Population dynamics of Virginia's hunted black bear population

by

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(ABSTRACT)

The Cooperative Alleghany Bear Study (CABS) was initiated in 1994 by the Virginia Department of Game and Inland Fisheries (VDGIF) and the Virginia Polytechnic Institute and State University (VPI&SU) to investigate population dynamics on Virginia's hunted bear population. CABS personnel handled 746 different bears (1.5M:1F) 1,368 times on its northern study area during June 1994 to September 2000. The sex ratio for summer captures was 1.5M:1F, which differed from 1:1 (n = 1,008, Z = 6.17, P < 0.0001). Sex ratios for the summer captures ranged considerably among years ($\chi2$ = 23.92, df = 6, P = 0.0005) and among age classes ($\chi2$ = 119.22, df = 4, P < 0.0001), with the largest discrepancy among yearlings (5.7M:1F). The sex ratio among captured adults favored females (0.6M:1.0F). Average age for all captured bears was 3.87 ± S.E. 0.12 years; females (n = 309) averaged 5.20 ± S.E. 0.16 and males (n = 402) averaged 2.84 ± S.E. 0.14 years (t = 10.92, df = 709, P < 0.001). Litter size averaged 2.35 cubs / litter over the 6-year period and sex ratio did not differ from 1:1 (n = 183, Z = 0.74, P = 0.461), but varied among years (χ^2 = 16.61, df = 5; P = 0.005).

Three-hundred-and-seventy-six (164M, 212F) of 746 captured individuals were equipped with radio-transmitters. The ratio of radio-collared bears fluctuated from 2.6 F:1M (1998) to 8.6F:1M. We tested a radio-collar effect on survival as a covariate and found a significantly higher survival for radio-collared adult and 3-year-old females in the first 3 years of the study (χ^2 = 6.64, 1 df, P = 0.01). Estimates using the Kaplan-Meier staggered entry showed survival rates for females (adults = 0.993, subadults = 0.997) higher than for males (adults = 0.972, subadults = 0.917). Estimates using the mark-dead recoveries data showed survival rates of 0.840 for adult females (0.714 for 2-year-olds) and 0.769 for adult males (0.335 for 2-year-olds).

We observed 34 mortalities of radio-collared bears for which hunting mortality accounted for 85%. Four natural mortalities included a 5-year-old female and a 2-year-old male that were killed by other bears, and a 14-year-old and 2-year-old female that died of unknown causes. Among the ear-tagged sample, 2-year-old males experienced the highest mean harvest rate of 45%, with a high of 65% mortality in 1996. Among females, 2-year-olds were most vulnerable with a harvest mortality rate of 22% a year.

Population modeling indicated that population growth rate of black bears in Virginia is most sensitive to changes in adult female reproduction and survival. With current survival and reproductive estimates, simulation indicated that adult female harvest has to increase 44% from current levels to stabilize population growth.

Population size estimates using Bowden's estimate for mark-resight data for a 100 km^2 sub-area on the northern study area ranged from 83-131 animals during 1998-2000. When adjusted for the proportion of time radio-collared bears spent on the study area population estimates fell to 63-96 bears. Using the Lincoln-Petersen estimate with Chapman's modification, black bear population estimates for the northern study area ranged from 582-1,026 animals during 1994-1999 on the 860 km^2 area.

Visitation rates to bait station sites correlated well with changes in population size estimates (n = 5, r = 0.97, P = 0.007). Black bear harvest in general was weakly correlated to change in population size (n = 6, r = 0.49, P = 0.328), however, archery harvest was highly correlated (n = 6, r = 0.95, P = 0.002). The monitoring indices showed all showed the same trends. We recommend a combination of them rather than relying on only a single index for monitoring Virginia's black bear population.

During winters 1995–2001, located 215 dens of radio-collared bears; 68% were in trees. Ground dens used by bears included nests in laurel thickets, excavations, brush piles, and rock cavities. The proportion of bears using tree dens did not differ between our 2 study areas (n = 203, χ^2 = 1.63, 1 df, P = 0.202), the proportion of females using tree dens (65%, n = 127) was greater than that of males (33%, n= 15; χ^2 = 10.69, 1 df, P < 0.001) on the northern study area. Sex and age were significant factors in determining the type of den a bear selected. Twenty-six of 66 individual bears handled for 2–6 consecutive years consistently used tree dens, 8 were faithful to rock cavities, and only 4 regularly used ground dens for denning. Twenty-eight bears (42.4%) switched den types over the 6–year period, primarily from tree dens to rock cavities.

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Many people have assisted with this study and with moral support, without which I doubt I would be writing this today. First, I would like to thank my major advisor and mentor, Dr. Michael R. Vaughan, for having faith in my capabilities; for always being open to all my questions, cries for help, and for cheering me up on my not-so-good days; for being my family while mine was far away; and for being a great friend that I will miss when I leave. My thanks go out to my graduate committee for their time and enthusiasm to help me in this process. I would like to thank Dr. Jim Berkson for his enthusiasm and help with the modeling work, his invaluable advice and mentoring for job-hunting, and his cheerful attitude around students. Dr. Dean Stauffer has always had an open ear for bouncing off ideas and helping me evaluate data. I thank Dr. Don Orth for keeping me on track with my objective and keeping a focus on the dissertation. Rich Oderwald has stimulated my professional thinking, especially with his preliminary exam questions.

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In addition, this project was supported by the uncountable hours of volunteers who have given part of their lives to make this study a success. CABS would not be able to achieve all its goals without the dedicated help of these volunteers. Specifically, I would like to thank my first German volunteers Kostja Geitner and Bernhard Helm. Joanna Schoenenberger from Switzerland and Julie King will be remembered for their cheerful personalities and hard work. Liz Baillie, from Scotland, and Pat Sharkey are remembered for their efforts to make the hair and camera studies a success.

This project would not have been possible without the enthusiastic commitment of VDGIF personnel, who assisted on different aspects of the project throughout the years. I would like to thank Jerry Blank for his unyielding commitment to black bears in Virginia. Jerry has taught me how to appreciate Virginia's wildlife and resources, has made me a decent trapper that can catch some 'ole – females', has given me the courage to dart my first bear in a tree, and has taught me how to cut with a chainsaw while hanging from a rope. He will always be a good friend and mentor. Thanks!

Denny Martin and his wife Carol have been great supporters of this project and without them the wheels would not be turning. Al Bourgeois, Oliver Burkholder, Fred Frenzel, Joe Huffer, David Kocka, Nelson Lafon, Bill Mohler, John Pound, Ben Powell, Roger Propst, Kenny Sexton, Gene Sours, Roy Swartz, and Wayne Lee Zollman invested countless hours in trapping and handling bears with us in the summers, and assisting during all the numerous side projects such as hair traps, camera surveys, etc. Thanks

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Finally, I am grateful to my Mom and Dad for making my dreams possible, for always having faith in my abilities, and for having made me the person that I am. To my fiancé, William Penhallegon, I cannot fully express my thanks for all his moral support during this process, spending his weekends out in the field when I had to work just to be with me, and for always having faith in me. I will always love you and look forward to a long life together.

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INTRODUCTION

Citizen groups throughout the country during much of the last decade have criticized hunting black bears (*Ursus americanus*), particularly hunting with dogs, over bait, and spring hunting. Loker and Decker (1995) reported that citizen groups focused on 3 major issues concerning the use of hunting as a population management tool: (1) insufficient knowledge about bear population parameters and individual biology, (2) ethical issues regarding bear hunting practices such as using hounds and hunting over bait, and (3) the conflict of interest between hunting groups and animal rights activists. Presently, public referenda have forbidden the use of hounds in Massachusetts, Oregon, Washington, Colorado, and Maryland. Also, bear hunting was stopped by the state court in California and by the state government in Florida due to lack of knowledge of black bear population levels and reproduction (Burton et al. 1994, Koch 1994).

To avoid a similar situation in Virginia as in the above states, the Virginia Department of Game and Inland Fisheries (VDGIF) and Virginia Polytechnic Institute and State University (VPI&SU) initiated a research project, the Cooperative Alleghany Bear Study (CABS), on Virginia's hunted bear population in 1994. Several bear studies in Virginia during the 1980s and 1990s focused on bear populations in protected areas such as Shenandoah National Park (SNP), Great Dismal Swamp NWR, and Mt. Rogers Recreation Area (Carney 1985, Comly 1993, Garner 1986, Hellgren 1988, Kasbohm 1994, Schrage 1994). Prior to CABS, information on Virginia's hunted bear population was limited. VDGIF began marking bears in 1957 (Strickley 1961), but did not obtain information on reproductive and survival rates, non-hunting mortalities and denning ecology. CABS has attempted to fill this information gap by focusing on demographic data such as cub survival, age structure, inter-birth interval, litter size, denning ecology, and causes of mortality (Godfrey 1996, Higgins 1997a, Ryan 1997).

The black bear is an important big-game species in Virginia with considerable public interest in its welfare and continued existence (Martin and Steffen 2000, Wright 2000). Bear hunting in Virginia, where hunting with dogs has a long tradition, has not been formally challenged by animal rights activists. CABS has collected information on hunter dynamics in Virginia (Higgins 1997b), which would be useful in the event of a challenge. In addition, the black bear in Virginia is an important big-game species that generates an undetermined amount of revenue for regional economies. It is therefore important to have as much knowledge about population size, reproduction and mortality rates for black bears as possible so that public concerns about bear hunting can be properly addressed.

The state's black bear population supports a several million dollar recreational industry with 95% (1997) and 93% (1998) of reported black bear harvests taken by Virginia residents (Wright 1989, 2000)VDGIF, unpublished data). The black bear harvest in Virginia is presently managed by setting hunting season length, bag and weight limits, controlling access to public lands, and regulation of hunting methods (different season for archery, still hunt and dog hunt; Martin and Steffen 2000). The number of big game licenses {deer (*Odocoileus virginianus*), bear (*Ursus americanus*), turkey (*Meleagris gallopavo*)} sold is not limited and is therefore not a valuable management tool. The number of bears harvested in the last 20 years has fluctuated, but is generally on an increasing trend particularly since 1992 and has tripled between 1990 and 1999 (Martin and Steffen 2000). Harvest records in Virginia date from 1947, but age-specific data have been collected only since 1982 when VDGIF first asked hunters to submit a premolar from harvested bears (Godfrey 1996). Reliable data might only be available since 1991, when submitting a tooth to VDGIF became mandatory (Godfrey 1996).

It is unclear if this increase in harvest can be attributed to an increase in bear population size or other factors, such a higher hunting success rate of individual hunters. All big-game license holders can legally take bears during 4 weeks of the deer archery season (late October-early November), for one week during the deer rifle season (late November) and during the bear firearm season in December.

Harvest rate, currently unknown and a main objective of this project, is one parameter essential to manage bear populations effectively. We also need to identify other factors that are important to managing Virginia's bear population. Possible factors include (1) bear population size, (2) harvest rates, (3) hunting pressure, (4) recruitment rates, (5) environmental impact on recruitment rates, and (6) cultural and intrinsic carrying capacities. This study was designed to summarize and add to existing data and complete the following objectives.

1. Estimate density, population growth rate and trend, reproductive and harvest rates for Virginia's hunted black bear population.
2. Illustrate den-type use and fidelity of Virginia's hunted black bear population.
3. Determine which demographic variables have the greatest influence on the growth rate of Virginia's hunted black bear population.
4. Evaluate the efficacy of several population monitoring techniques (e.g., bait station survey, camera mark-re-sight, bow hunter survey, car collision statistics, damage statistics) to accurately predict black bear population trends in Virginia.
5. Develop a mathematical model for Virginia's hunted black bear population, which will predict the responses of the population to environmental perturbations and management actions.

With these objectives completed, I want to provide a basic demographic analysis of Virginia's hunted black bear population to aid future management decisions. The population model will shed light on potential management options for hunting harvest changes.

STUDY AREAS

The Cooperative Alleghany Bear Study (CABS) has 2 study areas, one in northwestern, and the second in southwestern Virginia, established in 1994 and 1995 respectively (Fig. 1).

Northern Study Area

The northern study site is centered in Augusta and Rockingham counties, but includes portions of Highland, Bath, Allegheny and Rockbridge counties (Fig. 1). The area is dominated by Shenandoah Mountain, Elliot's Knob, and Great North Mountain and comprises 860 km^2 with elevations ranging from 480m at the base of Little North Mountain to 1,360m atop Elliot's Knob (Higgins 1997a, Kozak 1970). The majority of the site lies in the Dry River and Deerfield Ranger Districts of the George Washington and Jefferson National Forest (GW&JNF). Devonian and Mississippian sandstones and shale of the Pocono and Hampshire Formations dominate the well-drained bedrock (Rawinski et al. 1994).

Average yearly temperature reaches 10.9°C (1997-2001) at the center of the study area with average temperatures of 1.2°C in January and 20.8°C in July (Appalachian Cooperative Grouse Research Project, unpublished data). Average yearly precipitation reaches 79cm, mainly during April to September, and average snowfall of 67cm per year (National Oceanic and Atmospheric Administration, public data 1997-2001).

Dominant tree species include eastern hemlock (*Tsuga canadensis*), chestnut oak (*Quercus prinus*), red oak (*Q. rubra*), white oak (*Q. alba*), and tulip poplar (*Liriodendron tulipifera*). Common understory species include rhododendron (*Rhododendron maximum*) and eastern mountain laurel (*Kalmia latifolia;* Godfrey 1996 and Higgins 1997*a*).

Southern Study Area

The southern study area (1,544 km^2) is centered around the Mountain Lake Wilderness Area in Giles county on the Blacksburg and New Castle ranger districts of the GW&JNF (Fig. 1). It also accounts for portions of Montgomery and Craig counties (Ryan 1997). This part of the GW&JNF is highly fragmented by private land, which mainly lies at the valley bottoms (Higgins 1997*b*). Elevation rages from 492m in the Craig Creek drainage to 1,378m at Bald Mountain in the Mountain Lake Wilderness. Well-drained mountain bedrock is dominated by sandstone and shale (Soil Conservation Service 1985). Average annual temperatures were 7.6˚C at Mountain Lake Meteorological Station, ranging between –23.8˚C and 29.2˚C. Precipitation totaled 153cm in 1996, with monthly ranges between 7cm to 246cm (Ryan 1997).

Important tree species are similar to the Northwest Study Area, but also include red maple (*Acer rubrum*), pitch pine (*Pinus rigida*), and eastern white pine (*P. strobes*; Ryan 1997).

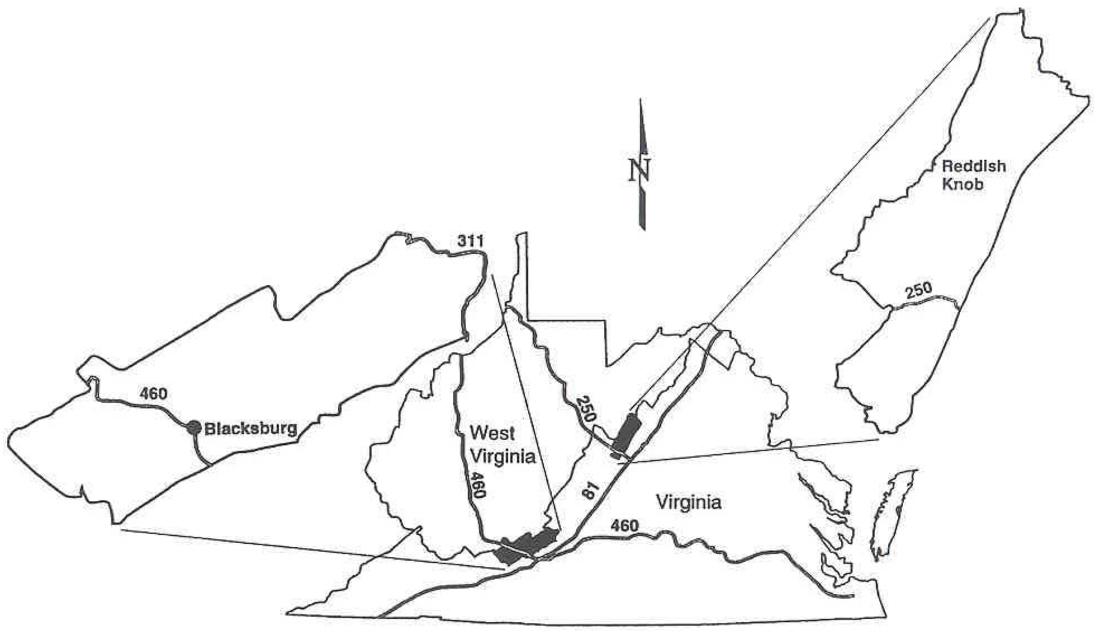

Figure 1. Northern and Southern study areas of the Cooperative Alleghany Bear Study, George Washington and Jefferson National Forests, Virginia, during 1994–2001.

LITERATURE REVIEW

Hunting constitutes 34–100% of black bear mortality in North America (Bunnell and Tait 1985, Elowe and Dodge 1989). Bunnell and Tait (1980) identified natality and mortality rates as the most important factors in black bear population dynamics, which should be considered by managers. However, survival and mortality rates other than harvest are poorly documented in the literature (Eberhardt 1990, Schwartz and Franzmann 1992). Adult female survival has been identified has the main factor influencing black bear populations (Eberhardt 1990). Therefore, many bear studies have focused on females and their reproductive parameters. Female survival estimates have mainly been obtained by monitoring radio-collared adult bears.

Estimates of mortality rates for bears are often limited to harvest data and hunter tag return. More accurate estimates of mortality, especially natural mortality, can be calculated from radio-marked bears (Carney 1985). Bear hunting mortality usually affects subadults and adults males more than female adults, due to their increased home range size, dispersal and trophy size (Bunnell and Tait 1980). LeCount (1987) hypothesized that male survival can become an important factor in heavily exploited populations due intraspecific predation of cubs and females by dispersing non-resident males. Female mortality may increase with increased hunting pressure; as the proportion of adult males declines, females may be more likely to be harvested (Bunnell and Tait 1985). Cub survival is also poorly documented, because they make up a small proportion of the harvest (Bunnell and Tait 1980). Survival rates are often based on observational data (i.e., presence of cubs in dens for consecutive years). Carney (1985) and CABS (unpublished data) reported capturing adult bears that had been assumed dead since they had not been observed in the den with their mother for 2 consecutive winters.

Yearling (12-24 months old) and subadult (2 and 3 year-olds) survival are also poorly documented by telemetry data. Difficulty in fitting these fast-growing animals with radio collars has contributed to the problem (Higgins 1997*a*). Monitoring of these age-classes is also complicated by dispersal, which can include great distances. Schwartz and Franzmann (1992) identified human-induced mortality as the major influence on dispersing subadults, however, they noted that females were 2-3 times more likely to survive to adulthood than males.

The management of wildlife and what types of data are needed is often debated in the literature. Researchers argue about how detailed data should be to be used as an effective management tool (Roseberry and Woolf 1991). Hayne et al. (1984) argued that it is often sufficient to know only a population's position in relation to carrying capacity and if it is increasing or decreasing. Others rely on modeling of populations as an essential management tool (Gross 1972, Pojar 1981). Roseberry and Woolf (1991) argue, however, that managers should verify and validate models with independent assessments of population status. Harvest data often are a manager's primary source of information for population management (Roseberry and Woolf 1991). They compared different techniques for analyzing harvest data and determined that population reconstruction was the simplest, most logical and accurate method to track population trends. Godfrey (1996) used this method for Virginia's existing harvest data and cautioned that Virginia's harvest data might be biased towards older males before 1991, when submitting a tooth to VDGIF became mandatory. Before that time, hunters might have been more likely to submit a tooth of a large trophy male than smaller bears. Godfrey (1996) also pointed out that a weakness of reconstruction is that it cannot be used to determine present trends or analyze harvest during the most recent years. Large data sets are needed in this analysis and do not provide recent trends, in which managers are often most interested. Population reconstruction should therefore be supplemented by other means of trend analysis.

Where accurate population data to estimate density are lacking due to time or budget constraints, population monitoring or trend analysis are necessary options. Direct counts and accurate population density estimates are difficult to achieve. Both are very expensive and time-consuming (Carlock et al. 1983). Many states, therefore, use indices to monitor population changes. Indices should be easily applicable and relatively inexpensive (Abler 1988). To ensure the accuracy for predicting population changes by an index, the index has to be compared to known population sizes over an extended period of time (Carlock et al. 1983, Davis and Windstead 1980). Anderson et al. (2001) pointed out that a risk in data analysis exists when sample size (*n*) is small relative to the number of parameters being estimated.

Track counts (Abler 1988), black bear damage indices (Carlock et al. 1983), sighting indices (Pharris 1981), and bear scat indices (Matthews 1977) have been shown to be weakly correlated with population size fluctuations. Pre-bait visitation rate in areas with regular and extensive trapping was a reliable monitoring method in Arkansas, but expensive and labor intensive (Smith 1985).

Johnson (1992) reported that bait station indices correlated well with the Jolly-Seber population estimates from Great Smoky National Park (GSMNP). Bait stations are used in several southern states and have proven to be an economical and valid index of relative black bear numbers (Johnson 1992, Kohn 1982). Preliminary results from van Manen et al. (unpublished report) indicate that a more comprehensive analysis of the bait station index used in GSMNP might not prove to be very valid, but they concede that that might be caused by the data collection technique. All bait stations in the National Park are located on mountain ridges that might miss the true population trend. Miller (1993) reported that bait station surveys low black bear density areas of in southern Mississippi were not successful due to low visitation rates. Roseberry and Woolf (1991) suggested a combination of indices, models and periodical estimates of population size to validate trends.

Many wildlife studies use a Jolly-Seber open population estimate to assess population size. Lint et al. (1995) used the modified Buckland (1980) model for capture-recapture data to estimate turkey population size. Buckland (1980) developed an extension of the Jolly-Seber estimate that includes known deaths as part of the recapture sample. Since many bears are known to die from harvest, this might be an important aspect to include into population estimates. Inclusion of harvest data would increase sample size and reduce standard errors of the population estimate (Lint et al. 1995).

Few population models specific to bears have been designed (McLaughlin 1998). Knight and Eberhardt (1984) and Shaffer (1983) built models to project grizzly bear (*Ursus arctos*) population size. Harris et al. (1986) developed a stochastic population model for animals in general and used it to simulate grizzly bear population dynamics. Taylor et al. (1987) designed a model (ANURSUS) to estimate population parameters for the North American bear species, which uses age-specific observations of litter size. McLaughlin (1998) developed a stochastic population model simulating the effects of food and harvest on female black bears in Maine. More recently, ESSA Technologies Ltd. (2001) developed a projection model based on life-table data for black and polar bears. It can incorporate Monte Carlo estimates of the uncertainty of similar results and in addition allows for density-dependent effects on all parameters specified.

None except McLaughlin's (1998) models include stochastic elements such as nutritional effects (e.g., lack of hard mast) on age of first reproduction and survival. Rogers (1976a) and Wathen (1983) suggested nutritional condition of cubs and yearlings determined their survival. The inclusion of this factor in a model might therefore be important to accurately predict population parameters for black bears. As mentioned above, in heavily exploited bear populations, mortality of males might influence reproductive rates of female black bears. Thus, it might be important for Virginia to include male population parameters in a population model.

GENERAL METHODS

Trapping and Handling

We began trapping bears in the northern study area in June 1994, and expanded to the southern area in June 1995. Trapping each year started in early June and continued until the end of August. The end of trapping season was dictated by the FDA regulation that bears cannot be immobilized with Ketamine / Rompun 45 days prior to the beginning of hunting season (FDA 2000). Animals were captured with Aldrich foot snares and culvert traps on trap lines selected to cover the whole study areas. Trap lines were pre-baited for 4-8 days before trapping began. Baits we used included doughnuts, pastries, meat scarps and scents (liquid smoke, molasses). We operated trap lines of 4–15 traps for 14 days at a time and then transferred to another line within the study area. Each trap site was located with the Global Positioning System (GPS). We recorded captures per trap site, number of trap nights, and number of bait nights.

We immobilized captured bears with a 2:1 mixture of ketamine hydrochloride and xylazine hydrochloride (concentration of 300mg/ml), delivered by jab sticks, blow pipes or dart pistols (Palmer Chemical Company, Douglasville, GA) at a dosage of 1cc per 44kg of estimated live weight. In most cases, xylazine was reversed by Yohimbine at 2cc per 44kg (concentration 5mg/ml). Animals were handled according to an approved protocol of the Virginia Tech Animal Care Committee (ACC# 98-069-F&WS).

We recorded weight (to the nearest kg), sex, reproductive status, injuries, and other body measurements. Physical condition was scored subjectively in the categories poor, fair, good, and excellent. We extracted the first premolar to determine age by cementum annuli analysis (Willey 1974). Blood and hair samples documented genetic relationships among individuals from each study site. Blood samples consisted of 2 10ml clot tubes, 2 10 ml heparin (anti-clot) tubes and 1 10ml tube containing ethylenediamine tetra-acetate (EDTA) for genetic analysis (Hellgren and Vaughan 1989b). Blood samples were stored in coolers in the field and were centrifuged immediately upon return to the office.

We examined females for lactation or signs of estrus (e.g., swollen vulva, discharge), and measured males' testicles to determine breeding status (Garshelis and Hellgren 1994). Similar measurements were taken on radio-marked bears in winter dens. We injected bears with a tetracycline antibiotic at 4cc per 44kg (concentration 200mg/ml) to prevent post-capture infections and to give the individual bears a marked cementum annuli that could be used in the mark-recapture analysis of the returned teeth during the bear harvest.

Marking Techniques

Each trapped bear received a metal (in 1994) or perma-flex plastic ear tag in each ear (since 1995) and a lip tattoo with the corresponding ear tag number. Some animals (mostly adult females) were fitted with a radio transmitter (ATS, Isant, MN; Lotek, Quebec, Canada; Telonics, Mesa, AZ; Wildlife materials, Carbondale, IL) that included a cotton breakaway device (Hellgren et al. 1988). Radio collars operated with a motion sensitive mortality mode (2 beats/second) on a 30-minute-delay schedule. Yearlings and large males received an ear tag transmitter (ATS, Isant, MN) starting in 1999 to avoid slipped collars (large males) or ingrown collars in fast-growing individuals. The ear-tag transmitters were on a 12-hour duty cycle (12 hours on – 12 hours off) to prolong battery life to 18 months. Cubs were marked with a lip tattoo and some cubs larger than 1.7 kg were fitted with expandable radio collars designed by CABS personnel (Higgins 1997*a*). The northern study area monitored 40-50 radio-collared animals per year, while the southern study area maintained about 30.

Radio Telemetry

We monitored radio-collared animals by triangulation with an H-antenna on the ground and by aerial telemetry. We attempted to locate each animal at least once a week and fly every other week for missing animals, den locations, and to locate mortalities/dropped collars. Triangulations on the ground consisted of 3 or more bearings from known locations (telemetry stations were located by GPS) within 30-minute time intervals. Each signal was rated by signal strength and confidence in the signal direction (Godfrey 1996). An overall rating was given to each ground location based upon activity of the animal, time, terrain and angle between bearings. We used telemetry locations for survival rate estimates, den locations, den entrance and emergence date, and litter size of females in dens.

Radio-collars for adult bears had a 30-minute and cub collars and implants a 4-hour delayed mortality switch. If a cub collar was detected on mortality, the cause was determined as soon as possible (e.g., death, dropped collar / transmitter). If a carcass was found, technicians and students attempted to determine cause of death in the field or bring the animal to the Department of Biomedical Sciences and Pathobiology of the Virginia-Maryland Regional College of Veterinary Medicine for necropsy.

Hunters in Virginia are required to check harvested bears at a registered check station. VDGIF and CABS offered a reward of 25$ for returned ear tags and 50$ for returned radio collars. Check stations were required to record ear tag numbers and tattoo numbers on a check card. Bear mortalities due to vehicle collisions were recorded when reported by Virginia Department of Transportation (VDOT), VDGIF game wardens or local police.

CHAPTER 1. POPULATION PARAMETERS OF VIRGINIA'S HUNTED BLACK BEAR POPULATION

Hunting constitutes 34–100% of black bear mortality in North America (Bunnell and Tait 1985, Elowe and Dodge 1989). Bunnell and Tait (1980) identified natality and mortality rates as the most important factors in black bear population dynamics, which should be considered by managers. However, survival and mortality rates other than harvest are poorly documented in the literature (Eberhardt 1990, Schwartz and Franzmann 1992). Adult female survival has been identified has the main factor influencing black bear populations (Eberhardt 1990). Therefore, many bear studies have focused on females and their reproductive parameters to evaluate population trends.

Estimates of mortality rates for bears are often limited to using harvest data and hunter tag returns, yet more accurate estimates of mortality, especially natural mortality, can be calculated from radio-marked bears (Carney 1985, Gese 2000). Bear hunting mortality usually affects subadult and adult males more than female adults, due to their increased home range size, dispersal and trophy size (Bunnell and Tait 1985). LeCount (1987) hypothesized that male survival can become an important factor in heavily exploited populations due to intraspecific predation of cubs and females by dispersing non-resident males. In addition, female mortality can increase with increased hunting pressure because females may be more likely to be harvested as the proportion of adult males declines (Bunnell and Tait 1985).

Cub survival is also poorly documented and makes up a small proportion of the harvest (Bunnell and Tait 1981). Cub survival rates are often based on observational data (i.e., presence of cubs in dens for 2 consecutive years). Carney (1985) and CABS (unpublished data) reported capturing adult bears that had been assumed dead since they had not been observed in the den with their mother for 2 consecutive winters. Yearling and subadult (ages 2 and 3) survival is poorly documented by telemetry data as well. Difficulty in fitting these fast-growing animals with radio collars has contributed to the problem (Higgins 1997*a*). Monitoring these age-classes is also complicated by dispersal, which can include great distances. Schwartz and Franzmann (1992) identified human - induced mortality as the major mortality influence on dispersing subadults (especially males) in hunted populations. They noted that females were 2-3 times more likely to survive to adulthood than males.

Accurate age-specific survival rates are necessary to understand population dynamics and for constructing a population model. Since reported hunter harvest of bears was Virginia's primary estimate for human induced mortality in the past, CABS used radio telemetry data to provide more accurate estimates of survival and causes of mortality (predation, starvation, disease, road kills, intra-specific predation). The objective of this chapter is to describe basic population parameters and demographics for Virginia's hunted black bear population, and identify causes of mortality.

METHODS

Capture ratios and demographics

We used the z-test for binominal proportions to test for differences in capture ratios for sex and age classes, and if total capture sex ratio differed from 1:1. To determine if mean age at capture differed between sexes we used a Students' T-test.

Reproduction

Reproductive characteristics (litter size, inter-birth interval, and age of primiparity) were determined from radio-collared females handled in dens and the female segment of our summer capture sample. Differences in litter size by age class and year were determined with χ^2 contingency tables.

Estimate of age- and sex-specific survival rates for radio-collared bears

CABS continually monitored 40-65 radio-collared bears (sex ratio 3:1 F:M) in the northern study area. Bears were classified in 5 age classes (cubs, yearlings, 2-year-olds, 3-year-olds, and adults) to determine age and sex-specific survival and mortality. Adults consisted of bears older than 3 years because, even though 3-year-old females give birth in Virginia, they often produce only one cub or lose their first litter (see results). We used 2 independent techniques to estimate survival rates. First, we used the Trent and Rongstad (1974) method modified by Heisey and Fuller (1985) in program MICROMORT 1.3. This method assumes constant survival rates within intervals and uses parametric estimation for its parameters. In addition, the Heisey-Fuller method assumes that survival times of individual animals are independent, that the sample is representative of the population being studied, and that all individuals within an age and sex class have the same mortality and survival probabilities during an interval. These probabilities can change among intervals (Heisey and Fuller 1985, Vangilder and Sheriff 1990). Interval survival rates were calculated for both sexes and the 4 age classes (Table 1), and pooled to an annual survival rate if the seasonal survival rates were not statistically different. MICROMORT offers a Z- test for comparing interval survival rates.

Survival estimates excluded a 7-day conditioning period to correct for behavioral changes that might affect the bear's survival. Bears were censored if they disappeared for 60 days (due to collar failure, emigration), or died within the first week of capture or due to handling in the den (Pollock 1982, Pollock et al. 1989). Censoring dates were the midpoint between the last record of an active signal and the first date not observed (e.g., 30 days after the last heard signal if not heard for 60 days). Mortality and dropped collar dates were determined by the midpoint between the last heard signal and recovery date of transmitters.

In addition, we used Kaplan-Meier's (1958) product-limit estimator modified by Pollock et al. (1989) to estimate survival for individuals in program MARK

Table 1. Survival intervals (example for the year 1999) for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Interval start	Interval end	Description	# days
28-Nov-1999	1-Jan-2000	Hound [1]	35
22-Nov-1999	27-Nov-1999	Rifle [2]	6
7-Nov-1999	21-Nov-1999	Hunting break	15
9-Oct-1999	6-Nov-1999	Archery season	29
26-Sep-1999	8-Oct-1999	Fall break	13
28-Aug-1999	25-Sep-1999	Chase [3]	29
27-Jul-1999	27-Aug-1999	Summer	32
1-Jun-1999	26-Jul-1999	Breeding season [4]	56
1-Apr-1999	31-May-1999	Den emergence	61
3-Jan-1999	31-Mar-1999	Den	88
			364

[1] bear hunting season, dogs permitted

[2] bear hunting season, dogs not permitted

[3] bear-dog training season

[4] The end of the breeding season was determined by the last day a female was captured showing signs of estrus, such as swollen vulva or discharge.

(White and Burnham 1995). The assumptions of the Kaplan-Meier method include 1) a random sample of marked animals; 2) radio-transmitters do not affect survival; 3) survival times were independent among individuals; 4) a censoring mechanism was random (i.e. mechanism is not related to fate of the animal); and 5) that newly tagged animals had the same survival probabilities as previously marked ones (Pollock et al. 1989).

Within MARK one can construct a variety of models such as pooling across years or age groups. Since we suspected different survival for the 5 age groups by sex, the input was stratified accordingly and modeled together at the same time to test for survival rate differences. One should construct plausible models *a priori* and select the most parsimonious model based on the Akaike's Information Criterion (AIC) values (Burnham 1993, Burnham et al. 1995, Chatfield 1995). AIC is an index of the balance of model parsimony and explanatory power related to the number of parameters. One can always achieve a 'perfect' model by over-fitting a model with many parameters (Burnham and Anderson 1998). In model selection one should chose the model with the lowest AIC value as the best model. In some cases there are several models that are plausible as the best model and they can be averaged for estimation of parameters based on a weighted average of the AIC values for the model (Burnham and Anderson 1998).

Estimate of age- and sex-specific survival rates for captured bears

We used summer captures and harvest returns to calculate age – and sex specific survival rates by 3 different methods. First, summer captures only were used in the standard Cormack-Jolly-Seber model (CJS; Cormack 1964). Trapped and marked animals are released into the population and are encountered by catching them alive and re-releasing them in succeeding summers; individuals can be encounter multiple times. In this model S_i is the probability of surviving the interval and remaining on the study area for subsequent captures. It is therefore labeled Phi(i) = S(i) – E (i), where E(i) is the probability of emigrating from the area. This estimate included both ear-tagged and radio-collared bears because the harvest bias does not influence our summer captures.

The second estimate of survival was derived from harvest returns of bears captured in the summer. As with the CJS, animals survive between occasions with the probability S(i). If one dies, the dead animal is reported with probability r(i) between capture occasions (Anderson et al. 1985, Anderson et al. 1993, Catchpole et al. 1995). This estimate was based on ear-tagged bears only.

The third approach is a combination of the 2 techniques discussed above. It allows the estimation of an animal's fidelity to an area [F(i) = 1 - E(i)] as the probability that the animal remains on the area and subsequently is available for recapture. This parameter allows the direct estimation of survival (S) rather than Phi(i) in the CJS (Burnham 1993). Since this estimate includes harvest returns it was based on ear-tagged bears only.

Assumptions of open mark-recapture models are (1) that the tagged population is representative of the population for which estimates are made, (2) that marks are not lost, misread or overlooked, (3) that all marking is done in a brief time period between intervals, (4) that the fate of an individual animal is independent (i.e., if a family group is marked, their survival might be dependent on one another), and (5) that every animal present in the population at the time of capture has the same probability of capture (i.e., equal catchability; Lebreton et al. 1992, Seber 1986)). The dead recovery analysis requires constant reporting rates over time and that all harvested animals are identified correctly (Lebreton et al. 1992).

Harvest rate

We calculated a direct harvest rate from bears that were trapped during the summer and harvested the following fall / winter. We separated harvest rates into sex and age classes and type of marking (ear tags only, ear tags and radio-transmitter) due to heterogeneity of capture probability, heterogeneity in harvest of male and female bears, and higher proportion of radio-collared female bears. Separate estimates were then combined for an annual harvest rate for the exploited bear population.

We excluded harvest of radio-tagged animals from this sample due to concerns of hunter bias. In meetings with the Virginia Bear Hunters Association (VBHA), hunters expressed their reluctance to harvest female bears in general and especially with radio collars. Especially in the first years of the study, all captured female bears were marked with color-coded ear tags, with which the hunters were familiar (Higgins 1997*a*).

Starting in 1997, we increased the numbers of radio-collared males to detect if there was a hunter selection bias against radio-collared bears and especially females. If mortality rates for the radio-collared bears were lower than for the ear-tagged population, a bias would exist.

RESULTS

Sex Ratio and Age Structure of Captures

CABS captured 746 different bears (1.5M:1F) 1,368 times on its northern study area during June 1994 to September 2000. Summer captures amounted to 1,008, whereas winter captures totaled 359 (Fig. 2; Appendix 1). Annual summer captures ranged from 122 (1995) to 174 (1999), and were conducted between May 15 and August 26 each year. Overall trapping success was 10 trap nights / capture (10,112 trap nights / 1,008 captures = 10.1% success rate), but ranged from 6.2 (1994) to 15.9 (1999; Appendix 1).

The sex ratio for summer captures was 1.5M:1F, which differed from 1:1 (n = 1,008, Z = 6.17, $P < 0.0001$). Sex ratios for the summer captures ranged considerably among years ($\chi^2 = 23.92$, df = 6, P = 0.0005; Table 2) and among age classes (χ^2 = 119.22, df = 4, $P < 0.0001$; Table 3), with the largest discrepancy among yearlings (5.7M:1F; Table 3, Fig. 2). The sex ratio among captured adults favored females (0.6M:1.0F; Table 3).

Average age for all captured bears was 3.87 ± S.E .0.12 years; females (n = 309) averaged 5.20 ± S.E. 0.16 and males (n = 402) averaged 2.84 ± S.E. 0.14 years (t = 10.92, df = 709, $P < 0.001$). Sample size for age is different than captures because some bears did not have a tooth removed for aging. Age of capture ranged from 0 to 20 for females and 0 to 18 years for males. Summer captures differed from the expected stable age distribution ratios in each age class for the younger bears (Fig. 2 and 3). The stable age distribution was calculated from capture and survival data of this project, as projected into the future with a Leslie Matrix (see Chapter 5). Age classes underrepresented in the summer captures include cubs and yearlings of all age and sex classes and 2-year-old females. Thirty-nine percent of all captures were adults (Fig. 2).

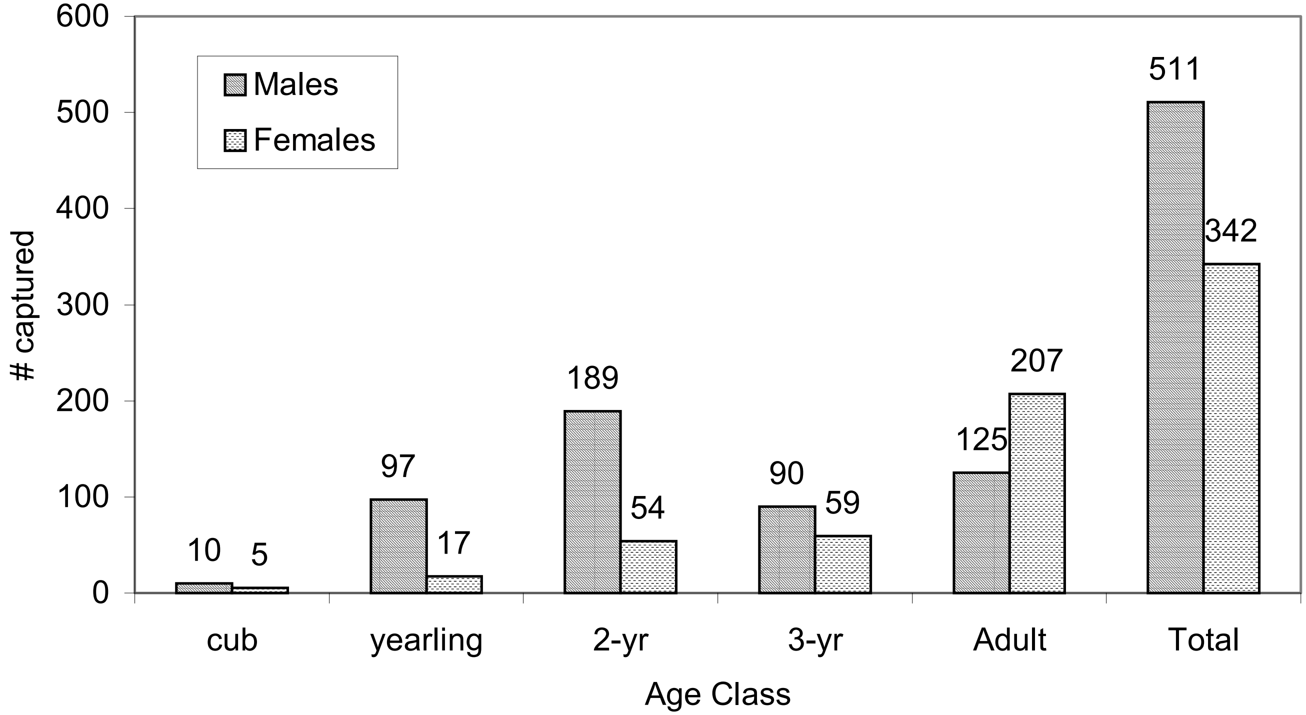

Figure 2. Sex ratio by age class of black bears captured during summers 1994-2000 on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Table 2. Sex ratios and Z-test for binomial proportions for black bears captured during summers 1994-2000 on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Year	*n*	Sex Ratio (M:F)	Z-value	P-value
1994	134	2.6 : 1	5.25	<0.0001
1995	122	1.8 : 1	3.49	0.0002
1996	138	1.5 : 1	2.19	0.0140
1997	157	1.1 : 1	0.56	0.2800
1998	149	1.5 : 1	1.79	0.0370
1999	174	1.5 : 1	2.4	0.0004
2000	134	1.1 : 1	0.66	0.1900
Total	1,008	1.5 : 1	9.3	< 0.0001

Table 3. Sex ratio by age class and Z-test for binomial proportions for black bears captured during summers 1994-2000 on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Age Class	*n*	Capture Sex Ratio	Predicted Sex Ratio [1]	Z-value [2]	P-value [2]
Cub	15	2.0M : 1.0F	1.0M : .1.0F	1.3	0.0984
Yearling	114	5.7M : 1.0F	1.0M : 1.0F	7.5	< 0.0000
2-yr	243	3.5M : 1.0F	0.7M : 1.0F	8.7	< 0.0001
3-yr	149	1.5M : 1.0F	0.4M : 1.0F	2.5	0.0055
Adult	332	0.6M : 1.0F	0.3M : 1.0F	-4.5	< 0.0001

[1] Population sex ratio predicted by model simulation in Chapter 5.

[2] Z-test performed on capture sex ratio.

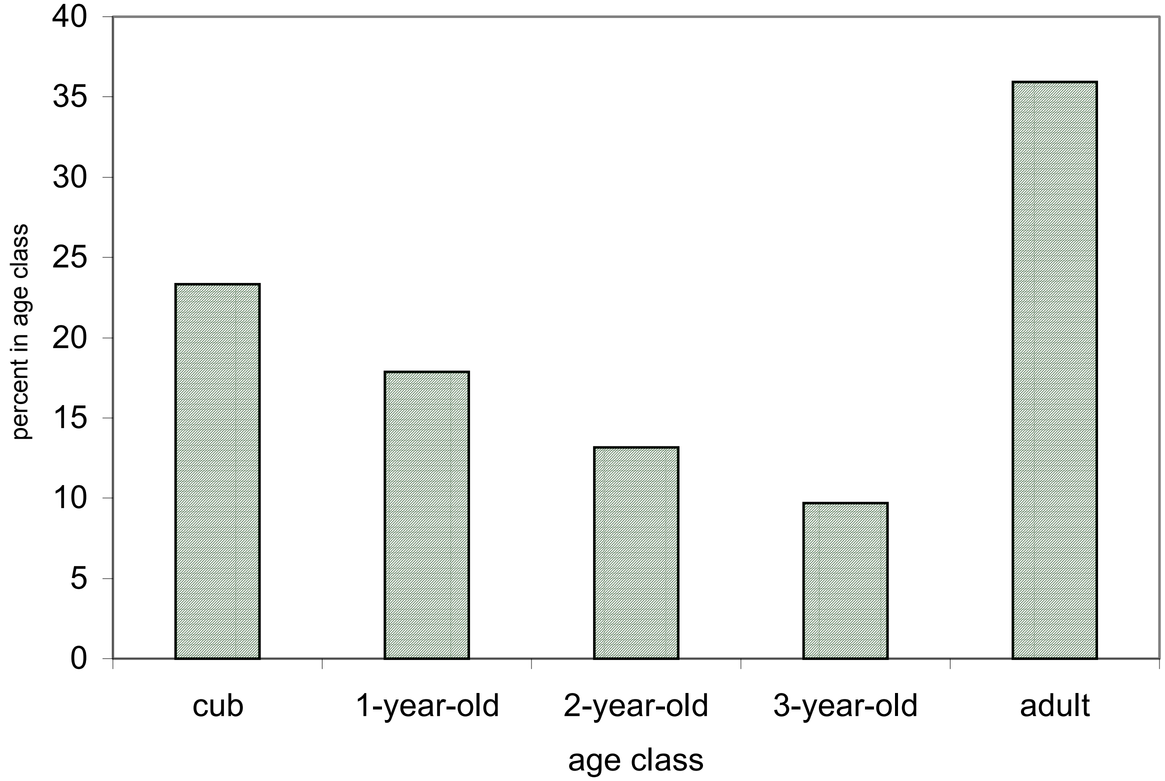

Figure 3. Stable age distribution of female black bears on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia, using survival and reproductive parameters estimated during this study (calculations see Chapter 5).

Reproduction

We handled 183 cubs in 72 litters including 86M:97F. The overall sex ratio did not differ from 1:1 (n = 183, Z = 0.74, P = 0.461), but varied among years (χ^2 = 16.61, df = 5; P = 0.005; Table 4). The skewed sex ratios among years did not seem to be related to mast production (r = -0.18, n = 6, P = 0.738; Table 4). The litter size most frequently observed was 3 cubs per litter, but varied among years (F = 3.83, df = 80, P = 0.004) and averaged 2.35 cubs / litter over the 6-year period (Table 5). Larger litters were found with older females, whereas younger females had none or mainly 1 cub (F = 7.29, df = 92, P < 0.0001; Table 6). In 2000, we had a record 3 of 8 litters with 4 cubs and the most distorted cub sex ratio of 2.3M:1F (Tables 4 and 5). Only females older than 6 years produced 4-cub litters (Table 6). Two of 156 females we captured > 5 years of age did not show signs of estrus, lactation or teat development indicating previous parturition. The 2 females (ages 7 and 9) that did not reproduce by 5-years of age have been monitored over a 4-year period and never reproduced during that time. Sterility might account for this lack of reproduction.

We observed an average of 55% of all females attempted or handled in dens to produce cubs each year (Table 7). This proportion varied among years ranging from 35% in 2000 to 74% in 2001. The regular inter-birth interval of 2 years is therefore shortened to 1.8 years (interbirth interval = between cubs, because some females seem to lose their cubs and reproduced in consecutive years, raising the expected proportion of females with cubs over 50%. An average of 21% of females that were in the reproductive age (> 3 years old) did not reproduce, ranging from 14% in 1999 to 29% in 2000 (Table 7).

Survival Rates and Mortality Factors of Radio-collard Bears

Three-hundred-and-seventy-six (164M:212F) of 746 captured individuals were equipped with radio-transmitters. We attached transmitters to 122 cubs (65M:57F), 47 yearlings (26M:21F), 28 2-year-olds (12M:16F), 35 3-year-olds (11M:24F), and 144 individual adults (50M:94F). The ratio of radio-collared females fluctuated from 1M: 2.6 F (1998) to 1M: 8.6F (1996; Appendix 2). The annual proportion of radio-collared bears harvested ranged from 0.02 to 0.14 for adult females and 0.00 to 0.25 for adult males (Fig. 4). We observed 34 mortalities of radio-collared bears (excluding 9 handling

Table 4. Sex ratios of cub litters handled in dens during 1995-2000 on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Year	*n*	Sex Ratio	Oak mast index	Z-value [1]	P-value
1995	22	1M:1F	32.10	0.00	1.000
1996	30	2M:1F	21.80	1.83	0.068
1997	33	0.83M:1F	21.30	0.52	0.620
1998	30	0.50M:1F	31.10	1.82	0.064
1999	45	0.45M:1F	60.80	2.53	0.012
2000	23	2.29M:1F	45.10	1.88	0.071
Total	183	0.89M:1F		0.74	0.461

[1] z-test for proportions

Table 5. Distribution of litter size by year for female black bears observed in dens during 1995-2000 for the Cooperative Allegheny Bear Study Northwest, George Washington and Jefferson National Forests, Virginia. [a]

Year	Litter Size 1	2	3	4	Number of litters	Average litter size
1995	7	3	3	0	13	1.69
1996	5	7	6	0	18	2.06
1997	1	4	8	0	13	2.54
1998	0	4	6	1	11	2.73
1999	1	8	8	1	18	2.50
2000	1	2	2	3	8	2.88
Total	15	28	33	5	81	2.35

[a] Number of litters observed differs from Table 4 because some litters were observed but not handled and sex ratio could not be observed.

Table 6. Number of cubs by age of female (reproductively active) for black bears handled in dens during 1995-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

			Number of cubs / female				
Female age	n	$\bar{x}$ (S.E.)	0	1	2	3	4
< 3	11	0.55 (0.37)	5	6	0	0	0
4 - 6	36	1.50 (0.20)	10	7	10	9	0
7-10	29	2.48 (0.23)	5	1	8	10	5
11-15	16	2.56 (0.31)	1	1	3	10	1
> 16	1	3.00 (1.23)	0	0	0	1	0
Total	93	1.98 (0.14)	21	15	21	30	6

Table 7. Reproductive status of reproductively active female black bears (> 3 years) observed in winter dens during 1998-2001 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Year		Reproductive Status		
		Cubs	Yearlings	Barren [a]
	n	Proportion	Proportion	Proportion
1998	32	0.44	0.31	0.25
1999	29	0.69	0.17	0.14
2000	31	0.35	0.35	0.29
2001	27	0.74	0.11	0.15
Total	119	0.55	0.24	0.21

[a] barren females should have produced cubs that year due to observed estrus during summer capture or having had yearlings the preceding den season.

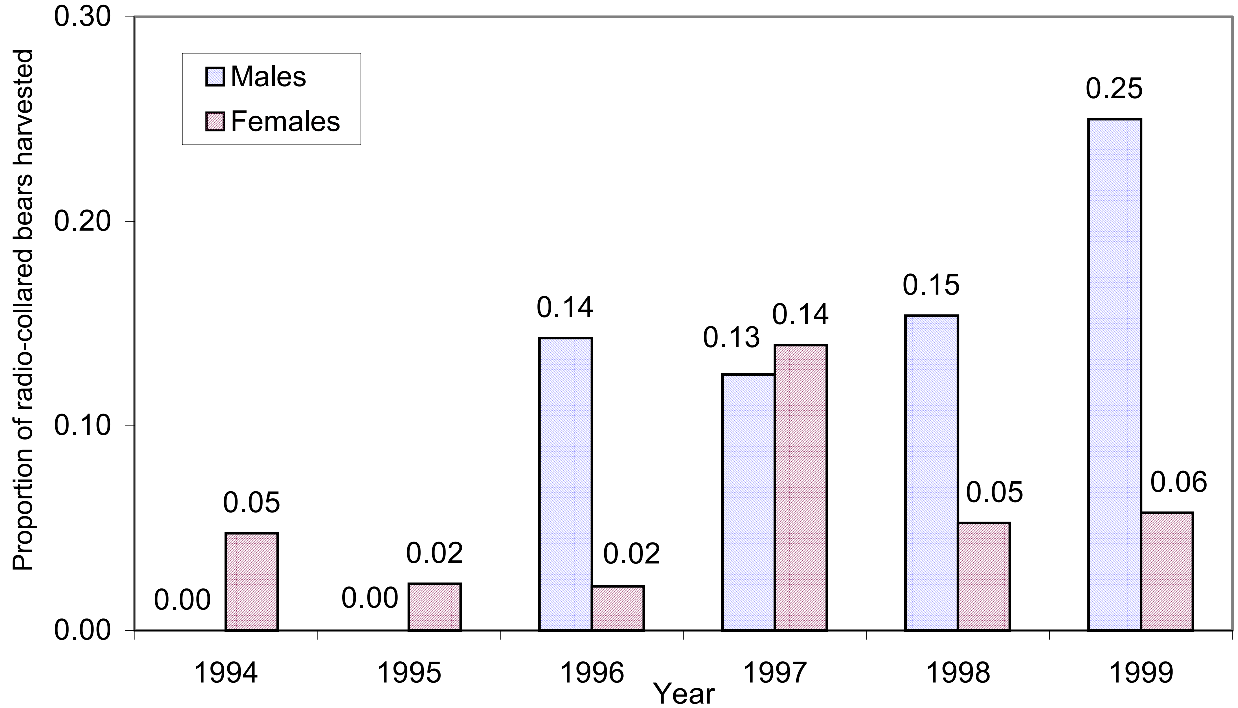

Figure 4. Annual proportion of radio-collared adult black bears harvested during 1994-1999 on the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

mortalities and all cubs) with hunting mortality accounting for 85.3% of all radio-collared (Table 8). All but 4 hunting mortalities (2 F: archery, 2 F: rifle) occurred during the hound-hunting season. Sex ratio of harvested radio-collared bears was 1:1 (13M:15F; Table 8). CABS experienced 9 handling mortalities (all female) during 1994-1999 (up to 2 / year), due mainly to suffocation in dens (n = 7). Three natural mortalities included a 5-year-old female and a 2-year-old male that were killed by other bears, and a 14-year-old female that died of an unknown cause.

I censored the 9 handling mortalities for the survival analysis, 4 subadult females and 9 subadult males due to dropped collars, 34 subadult females and 3 subadult males because they entered the adult age class, and 1 subadult female and 1 subadult male due to collar failure. In the adult age classes we censored 73 individuals (23M:50F) due to dropped collars, 4 males and 25 females because they reached the end of the study period, and 1 female due to collar failure.

Modeling survival rates using the Kaplan – Meier approach in Program Mark consistently showed that there was no annual variation. For all age and sex classes, models with annual variation showed low AIC values (Tables 9-12). For adult females, the best model included one pooled hunting season survival (0.976 95% C.I. 0.960 – 0.986) and the rest of the year constant survival (0.999, 95% C.I. 0.995 – 0.999; Tables 9 and 13). Subadult female survival was best modeled by one estimate (0.997, 95% C.I. 0.980 – 0.999) pooled across years and months (Tables 10 and 13). Modeling adult male survival favored estimating non-hunting survival (1.000, 95% C.I. 1.000 – 1.000), archery season survival (0.970, 95% C.I. 0.814 – 0.996), non-dog hunting season survival (0.800, 95% C.I. 0.621 – 0.907), and dog-hunting season survival (0.920, 95% C.I. 0.731 – 0.980; according to AICc values; Tables 11 and 13). Modeling subadult male (2 and 3 years old) survival showed that estimating non-hunting survival (1.000, 95% C.I. 1.000 – 1.000), archery season survival (0.933, 95% C.I. 0.648 – 0.997), non-dog hunting season survival (0.938, 95% C.I. 0.665 – 0.991), and dog-hunting season survival (0.500, 95% C.I. 0.260 – 0.740) were best supported (according to AICc values; Tables 12 and 13).

Table 8. Sources of mortality for radio-collared adult (> 3 year) and subadult (2 and 3 years) black bears handled between 1994-1999 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

			Mortality Source			
Year	Age Class	Sex	Hunting	Natural	Unknown	Total
1994	Adult	F	2	1	0	3
		M	0	0	0	0
	Subadult	F	0	1	0	1
		M	0	0	0	0
1995	Adult	F	1	0	0	1
		M	0	0	0	0
	Subadult	F	0	0	0	0
		M	3	0	0	3
1996	Adult	F	1	0	0	1
		M	1	0	0	1
	Subadult	F	0	0	0	0
		M [1]	--	0	--	--
1997	Adult	F	6	0	1	7
		M	1	0	0	1
	Subadult	F	0	0	0	0
		M	3	0	0	3
1998	Adult	F	2	1	0	3
		M	2	0	0	2
	Subadult	F	0	0	0	0
		M	2	1	0	3
1999	Adult	F	3	0	0	3
		M	2	0	0	2
	Subadult	F	0	0	0	0
		M	0	0	0	0
Total			29	4	1	34
Percent			85.3	11.7	3.0	100.0

[1] no subadult males collared during this time period

Table 9. Known fate survival models ordered by their AIC weights for adult female black bear radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Pollock et al. 1998).

Model	AICc	Delta AICc	AICc Weight	Number of Parameters
{Phi (pooled hunting season months, all others constant}	167.03	0.00	0.59	2
{Phi (pooled hunting season months individual, all others constant}	167.79	0.76	0.40	4
{Phi (pooled hunting season months}	176.76	9.73	0.00	10
{Phi (survival by months pooled across years}	177.55	10.52	0.00	12
{Phi (individual years)}	189.72	22.69	0.00	7
{Phi (constant across time)}	191.89	24.86	0.00	1

Table 10. Known fate survival models ordered by their AIC weights for subadult female (2 and 3 years) black bear radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Pollock et al. 1998).

Model	AICc	Delta AICc	AICc Weight	Number of Parameters
{phi(constant across all months)}	15.68	0.00	0.60	1
{phi (hunting months pooled across years, all others constant)}	16.75	1.07	0.35	2
{phi (individual hunting months pooled across years, all others constant)}	20.84	5.15	0.05	4
{phi (hunting months pooled across years, other months different)}	33.34	17.66	0.00	12
{phi (months pooled across years)}	37.68	21.99	0.00	14
{phi(t)}	167.86	152.18	0.00	66

Table 11. Known fate survival models ordered by their AIC weights for adult male black bear radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Pollock et al. 1998).

Model	AICc	Delta AICc	AICc Weight	Number of Parameters
{phi(pooled hunting season months individual, all others constant}	61.05	0.00	0.63	4
{phi(pooled hunting season months, all others constant}	62.13	1.08	0.37	2
{phi(survival by months pooled across years}	77.91	16.86	0.00	12
{phi(all months constant)}	84.60	23.55	0.00	1
{phi(pooled hunting season months, others individual}	84.76	23.72	0.00	10
{phi(individual years}	94.31	33.26	0.00	7

Table 12. Known fate survival models ordered by their AIC weights for subadult male (2 and 3 years) black bear radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Pollock et al. 1998).

Model	AICc	Delta AICc	AICc Weight	Number of Parameters
{phi(pooled hunting season months individual, all others constant}	42.62	0.00	0.96	4
{phi(pooled hunting season months, all others constant}	49.15	6.53	0.04	2
{phi(constant across time)}	64.17	21.55	0.00	1
{phi(survival by months pooled across years}	68.88	26.26	0.00	14
{phi(individual years)}	72.17	29.55	0.00	6
{phi(pooled hunting season, others different}	74.87	32.25	0.00	13

Table 13. Kaplan – Meier estimates of survival rate (95% C.I.) by interval for subadult (2 and 3 years) and adult black bears radio-collared between 1994 – 2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Pollock et al. 1998). Bold estimates are the best estimates from model selection according to AICc values (Tables 9-12).

	Age Class			
Interval	Adult Female (*n* = 21 – 52)	Subadult Female (*n* = 6 – 16)	Adult Male (*n* = 4 – 13)	Subadult Male (*n* = 1 – 7)
Year	0.993 (0.988 - 0.996)	**0.997 (0.980 - 0.999)**	0.972 (0.948 - 0.986)	0.917 (0.849 - 0.956)
Non-hunting season	**0.998 (0.995 - 0.999)**	0.995 (0.967 - 0.999)	**1.000 (1.000 - 1.000)**	**1.000 (1.000 - 1.000)**
Pooled hunting season	**0.976 (0.960 - 0.986)**	1.000 (1.000 - 1.000)	0.900 (0.815 - 0.946)	0.800 (0.658 - 0.893)
Archery hunting	0.990 (0.961 - 0.998)	1.000 (1.000 - 1.000)	**0.970 (0.814 - 0.996)**	**0.933 (0.648 - 0.997)**
Non-dog hunting	0.964 (0.927 - 0.983)	1.000 (1.000 - 1.000)	**0.800 (0.621 - 0.907)**	**0.938 (0.665 - 0.991)**
Dog hunting	0.973 (0.937 - 0.989)	1.000 (1.000 - 1.000)	**0.920 (0.731 - 0.980)**	**0.500 (0.260 - 0.740)**

Annual survival rates from the Kaplan-Meier approach were consistently higher than the Heisey – Fuller estimates (for annual survival estimates see Appendices 3 – 6). In general, confidence intervals of the Kaplan – Meier estimates were much smaller than the Heisey – Fuller estimates.

Subadult male survival rates could not be estimated in 1996 because none were collared and should be ignored for 2000 because it is based on one individual (Appendix 3). Subadult female survival was 1.0 in all but 2 years when one of the collared females was harvested (1994, 2000; Appendix 4). During 1994-2000 we monitored between 4-13 adult males at one time. Hunting was the only cause of mortality for this sex/age class. Survival rates were 1.0 for 1994 and 1995 when only 4 and 6 adult male bears were radio-collared. Only the subadult female group had mortalities (n = 2) outside the hunting season; one died due to handling and one of natural causes (Table 8). All other groups registered no mortalities during the non-hunting season.

Survival rates and mortality factors for ear-tagged bears

At least 277 of 746 (37.1 %) marked (radio-collared and ear tagged) bears died of known causes. Only 9 (1.2%) died of causes other than harvest. They included 5 road kills (5M:1F adults), 1 nuisance kill (M), 1 2-year-old male cannibalized by another bear, 1 3-year-old bear possibly poisoned or heat exhausted found next to a hunter bait site, and 1 bear that died of a ruptured spleen during a hunter chase in the bear-dog training season. All other mortalities (206M:62F) were caused by hunter harvest.

Survival estimates for all age classes by the 3 different approaches described in the Methods were similar, but lower than the survival estimates for radio-collared bears. All confidence intervals overlapped each other within age classes but we found a significant difference between age classes ($F = 13.77$, $df = 5$, $P < 0.001$). Adult and 3-year-old females had the highest survival rates, followed by 2-year-old females, adult males, and 3 and 2-year-old males (Table 14). Among the 3 estimates, the Cormack-Jolly-Seber (CJS) estimates produced the lowest survival rates for

Table 14. Comparison of estimated annual survival rates for black bears captured during 1994-2000 (excluding handling mortalities) for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia. The Cormack – Jolly – Seber estimate includes radio-collared bears because capture was not influenced by radio-collars.

Age class	Recapture rate	Cormack – Jolly – Seber		Dead recoveries		Burnham's combined model	
		Estimate	95% C.I.	Estimate	95% C.I.	Estimate	95% C.I.
Females							
Adult	0.281	0.838	0.751 – 0.898	0.840	0.687 – 0.926	0.812	0.691 – 0.893
3yr	0.417	0.838	0.751 – 0.898	0.840	0.687 – 0.926	0.812	0.691 – 0.893
2yr	0.530	0.564	0.336 – 0.768	0.714	0.410 – 0.900	0.812	0.691 – 0.893
Male							
Adult	0.435	0.620	0.491 – 0.734	0.769	0.555 – 0.900	0.673	0.517 – 0.798
3yr	0.513	0.461	0.378 – 0.547	0.565	0.328 – 0.775	0.673	0.517 – 0.798
2yr	0.521	0.461	0.378 – 0.547	0.335	0.220 – 0.474	0.365	0.268 – 0.475

subadult females 0.530, 95% C.I. 0.336-0.768). The dead recoveries estimate estimated subadult males the lowest (0.335, 95% C.I. 0.220-0.474). Recapture rates for adult females were only 28%, whereas all other age classes were around 40-50% (Table 14).

We tested a radio-collar effect on survival as a covariate (in Program MARK) and found a significantly higher survival for radio-collared adult and 3-year-old females in the first 3 years of the study in the dead recoveries analysis ($\chi^2 = 6.64$; df = 1; P = 0.01). The other 2 analyses did not detect a radio-collar effect.

Virginia black bear harvest, harvest rates, and hunter participation

Black bear harvest in Virginia was generally constant during 1928 - 1973, averaging 272 bears (Fig. 5; Martin and Steffen 2000). Hunting regulations changed in 1973, which closed hunting in 67 counties and shortened the hunting season by 2 weeks at the beginning of the hunting season (Martin and Steffen 2000). Harvest in the subsequent 7 years was slightly lower than the 1928-1973 period, but steadily increased starting in 1981 (Fig. 5). In 2000, Virginia bear harvest reached an all-time record of 1000 bears, a 368% increase from the average of 272 during 1928-1973. Average percent females taken declined from 46.4% (1963-1973) to 38.3% (1974-1998).

Harvest rates varied from year to year and among age classes (Table 15). If averaged across years (weighted mean), harvest rates were complementary to mortality rates calculated in the above section. Two-year-old males experienced the highest mortality rate of 45%, with a high of 65% mortality in 1996. Among females, 2-year-old females were most vulnerable with a harvest mortality rate of 22% a year. The overall average harvest rate for black bears on the northern study area was 30% a year (Table 15).

The trend of hunter participation and effort has been decreasing unlike total harvest. In 1973, Virginia registered an estimated 50,000 bear hunters whereas in 1999, Wright et al. (2000) reported 17,157 hunters. Similarly, hunter effort, which is measured in hunter-days (i.e., 8 hunter-days could be one person hunting 8 day or 4 persons hunting 2 days) decreased between 1993-1999 (Fig. 6). In general, there

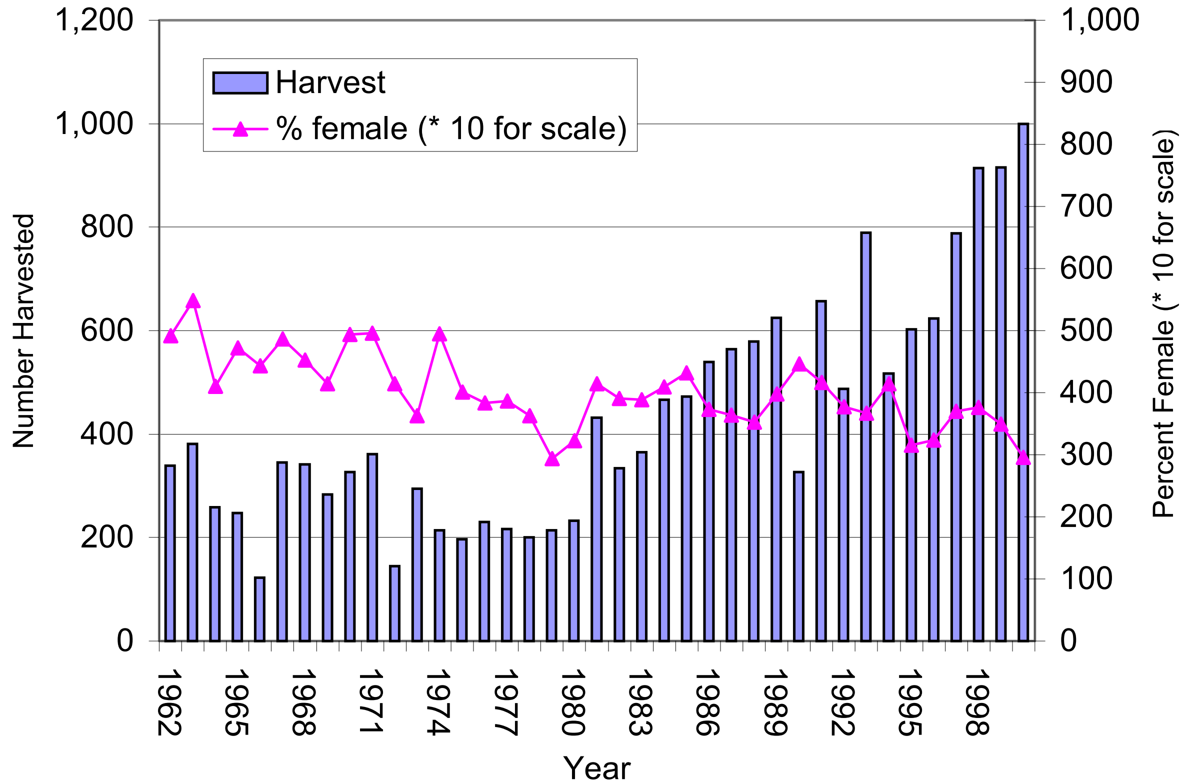

Figure 5. Virginia black bear harvest during 1963-1999 and percent female harvested. Hunting regulations were changed in 1973.

Table 15. Direct harvest returns of tags from bears tagged the preceding summer (excluding radio-collars) for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

	Year														
	1994	*n*	1995	*n*	1996	*n*	1997	*n*	1998	*n*	1999	*n*	N	Weighted Mean	S.E.
Age Class															
Adult Female	--	0	0.00	1	0.00	4	0.33	12	0.09	11	0.00	10	38	0.13	(0.07)
2yr Female	--	0	--	0	0.00	6	0.00	4	0.50	6	0.29	7	23	0.22	(0.12)
3yr Female	--	0	--	0	0.00	1	0.00	8	0.11	9	0.00	3	21	0.05	(0.03)
Weighted mean (S.E.)					0.00	(0.00)	0.17	(0.12)	0.19	(0.12)	0.10	(0.10)		0.13	(0.05)
n		0		1		11		24		26		20	82		
Adult Male	0.08	1	0.00	7	0.20	5	0.33	3	0.33	6	0.20	5	27	0.19	(0.06)
2yr Male	0.30	6	0.60	10	0.65	20	0.37	19	0.38	26	0.40	35	116	0.45	(0.05)
3yr Male	0.18	2	0.33	12	0.50	2	0.25	8	0.44	9	0.00	5	38	0.30	(0.06)
Weighted mean (S.E.)	0.25	(0.06)	0.34	(0.16)	0.56	(0.12)	0.33	(0.04)	0.39	(0.02)	0.33	(0.09)		0.38	(0.04)
n		9		29		27		30		41		45	181		
N		9		30		38		54		67		65	263		
Overall Weighted Mean	--	--	--	--	0.40	(0.11)	0.26	(0.05)	0.31	(0.05)	0.26	(0.07)		0.30	(0.04)

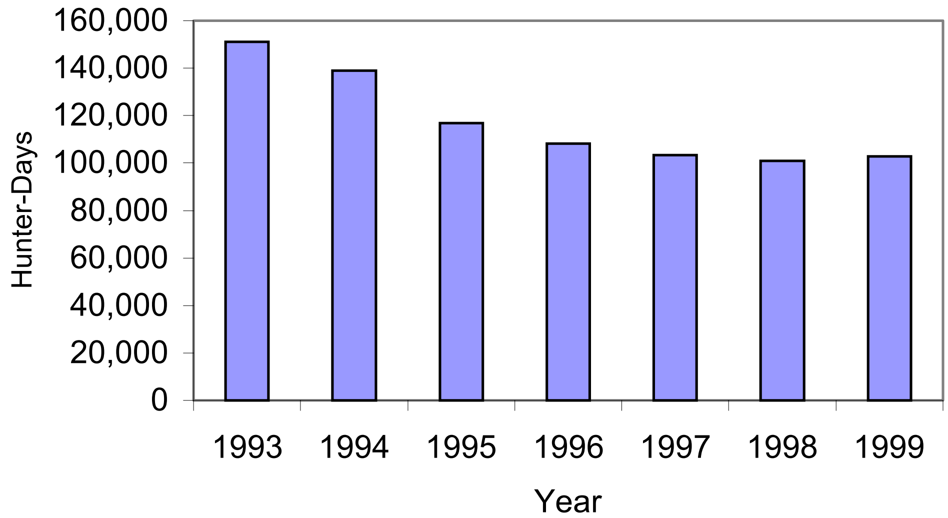

Figure 6. Hunter effort (measured in hunter-days: one hunter day = one hunter spending one day of hunting) of Virginia black bear hunters during 1993-1999 (data from Wright et al. 2000).

seems to be a negatively correlated trend between harvest and hunter effort (Fig. 7). Except in 1993, when 789 bears were harvested in 19,920 hunter-days, the trend is negatively correlated for 1994-1999 (with 1993 data point: $n = 7$, $r = -0.43$, $P = 0.330$; without 1993 data point: $n = 6$, $r = -0.83$, $P = 0.040$; see discussion for why 1993 is left out).

DISCUSSION

Hunting mortality represents a large proportion of adult black bear mortality in North America (Bunnell and Tait 1985). Virginia's black bear harvest has increased steadily over the last 20 years and is continuing its upward trend (Martin and Steffen 2000). Investigating population parameters and demographics is especially important for a species with a slow reproductive rate and can aid in achieving management goals of either stable, increasing or decreasing population levels.

Sex Ratio and Age Structure of Capture

Numerous black bear studies have reported sex ratio at capture that were skewed towards males (Harlow 1961, Hellgren 1988, Ryan 1997). Male black bears seem to have higher probability of capture than females due to large dispersal distances, larger home ranges (especially during breeding season in June and July), and later denning (Bunnell and Tait 1985). The relative vulnerability of males versus females could be related to the difference in home-range sizes (Bunnell and Tait 1985). Alt et al. (1980) reported home range sizes for black bears in Pennsylvania reaching 173 km^2 for males and 41 km^2 for females, leaving a potentially higher vulnerability of up to 4:1 for males (Alt et al. assumed linear relationship of home range versus vulnerability here). Consistent with heavily exploited populations, however, this higher capture vulnerability probably only applies to the younger age classes. Females experience higher survival rates in all age classes and more

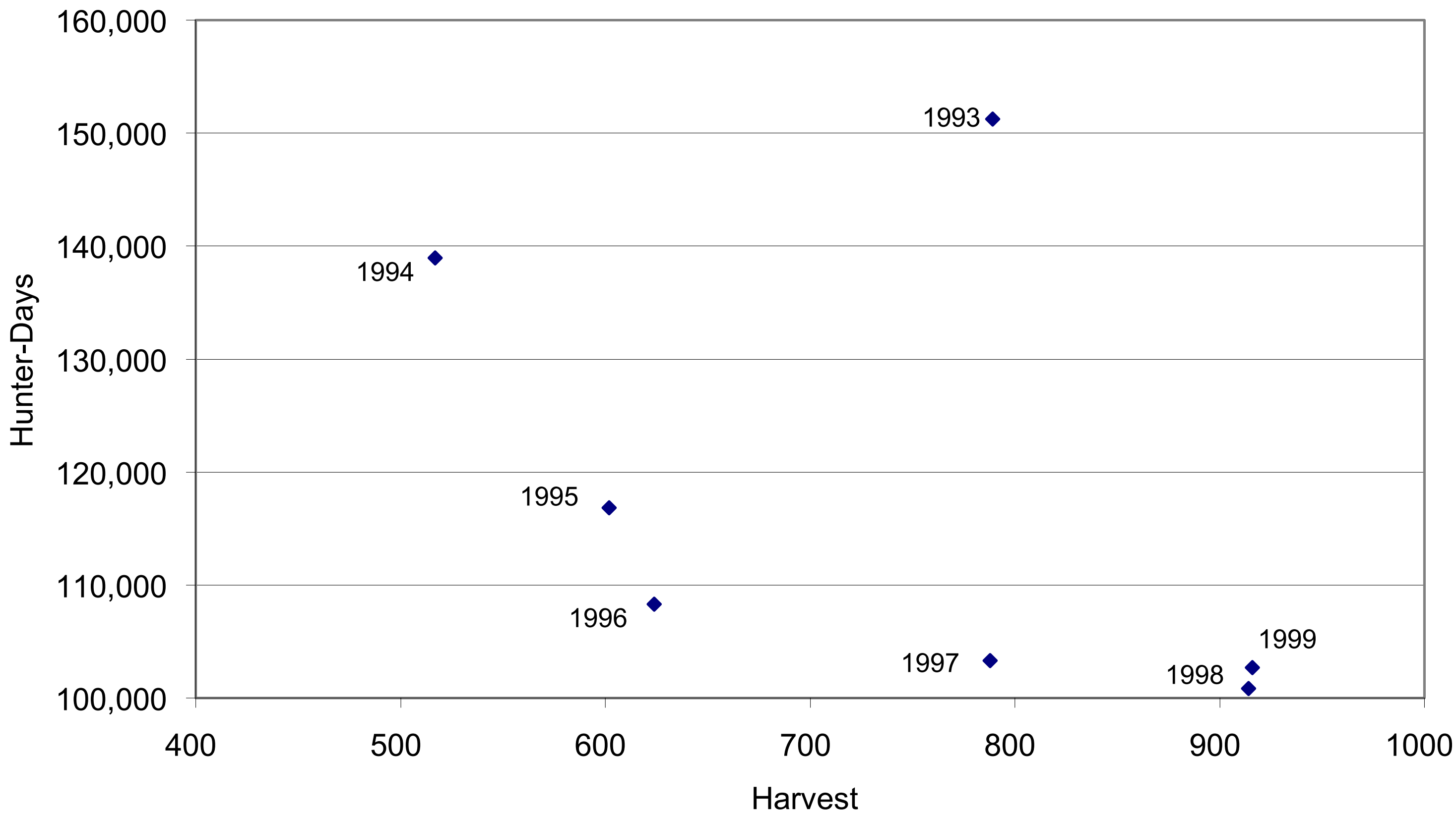

Figure 7. Hunter effort (measured in hunter days) versus total harvest for Virginia black bears during 1993-1999.

individuals reach the adult age class to be available for capture (Bunnell and Tait 1985). In this study, subadult sex ratio at capture was skewed towards males in this study, whereas adult captures were skewed towards females (0.6M:1.0F). Since females experience higher survival rates in all age classes, more individuals reach the adult age class and are available for capture.

Summer captures did not reflect the expected ratios in each age class for a stable age distribution, which is a prerequisite to constructing a valid life table analysis (Caughley 1977). Cubs, yearlings and 2-year-old females in particular were missing in our summer captures to represent the stable age distribution at capture (Figs. 2 and 3). Cubs and yearlings might be underrepresented because they are still with their mothers, who might encounter a trap before their offspring. Two-year-old females that have left their mothers to establish their own home ranges likely have very small home ranges, which also would minimize encounter with our trapping grids. Some of the trap lines can be up to 3 miles apart from each other, which might be further than the diameter of a subadult female home range. We found no published literature on subadult female home range size, but this parameter is currently being investigated by CABS. The fact that 2-year-old males are represented much more than females (3.5M:1F) in summer captures is probably related to their greater tendency to disperse and their higher mobility, which may increase vulnerability to capture (Bunnell and Tait 1985). Compared to other studies in Virginia, the proportion of adults (> 3 years old) in our summer captures (39 %) was low; Carney (1985) reported adult captures of 67 – 71% in Shenandoah National Park (SNP) during 1982-1984 and Kasbohm (1994) captured 50% adults in SNP. Bear populations that are hunted on a negligible level (like SNP) report 70% adults and a mean age of greater than 4 years old (Beecham 1983a, LeCount 1983, Young and Ruff 1982). In contrast, more intensively hunted populations (like the CABS study areas) report < 55% adults and an average age below 4 years (Beecham 1983a, Carlock et al. 1983, Jonkel and Cowan 1971). This discrepancy reflects that more individuals in protected populations may survive at a young age to be recruited into the adult age classes, which are then available for capture.

The average age of capture for males in this study was much lower than for females suggesting fewer older male bears (M: $\bar{x}$ = 2.84 ± S.E. 0.14; F: $\bar{x}$ = 5.20 ± S.E.

0.16). Compared to a life span of up to 30 years for bears this low average age may also be a sign of regular exploitation (Garshelis 1990). One could argue that the skewed mean age is due to the unequal probability of capture between adult females and subadult males. Even so, harvest data from Virginia also shows that males (< 3 years) constitute 72% of the total male harvest (average during 1978-1998), and are not reaching the older age classes to be captured (Martin and Steffen 2000). In addition, bear hunters in Virginia reported that they avoid harvesting females if they can identify the sex, which might contribute to a larger proportion of mature females in the population (Higgins 1997b).

Reproduction

Average litter size for this study (2.35 cubs / litter) corresponds with previous studies in Virginia, which ranged from 2.0 to 2.6 cubs per litter (Carney 1985, Hellgren 1988, Kasbohm 1994, Schrage 1994). Our findings correspond to other studies of litter size in the eastern United States, ranging from 1.4 to 2.3 cubs per litter in Arkansas (Clark and Smith 1994), 2.4 to 2.6 in Great Smoky National Park (Eiler et al. 1989), to 2.9 to 3.0 cubs per litter in Pennsylvania's unexploited population (Alt 1982, 1989). Western black bear populations report lower litter sizes on average, ranging from 1.9 cubs per litter in Idaho (Reynolds and Beecham 1980) to 1.3 to 2.0 cubs per litter in Yosemite National Park (Keay 1995). Litter size apparently increases with sow age (Alt 1989, Kolenosky 1990), a conclusion supported by our study. However, Needham-Echols (2000) observed that this trend can sometimes be lacking if poor mast years and nutritional condition prevent even experienced females from raising a litter. Noyce and Garshelis (1994) reported that litter size and age of first reproduction are good indicators of nutritional condition.

Sex ratio of black bear cubs is usually 1:1 (Alt 1981, Jonkel and Cowan 1971, Liu and Xiano 1986). We observed a high variability of sex ratio in cub litters between years (χ^2 = 16.61, df = 5; P = 0.005; Table 4), but it did not seem to be related to mast production (r = -0.18, n = 6, P = 0.738; Table 4). Sex ratio was skewed towards females in both good and poor mast years, however, the sex ratio was 1:1 overall (6 years). However, Noyce and Garshelis (1994) stated that the proportion of male cubs in a litter increased with increasing weight of the mother, but only in litters of 3 or fewer. Conversely, in Quebec, Samson and Huot (1995) did not find a relationship between proportion of male cubs in a litter and better nutritional condition of the mother.

Age of primiparity in this study (as investigated by Needham 2000 but not in this analysis) corresponds to other studies in the Eastern United States with bears often reproducing at age 3 and in some instances at age 2 (Alt 1981, Hellgren and Vaughan 1989a, McLaughlin et al. 1994, Ryan 1997). The age of primiparity is influenced by habitat quality, which in turn influences female nutritional condition (Beecham 1983b, McLaughlin et al. 1994). In poor mast years, bears in Maine failed to reproduce completely, driving the age of primiparity for that year's cohort up to 4 years of age (or older when consecutive failures were observed; McLaughlin et al. 1994). In Virginia, widespread mast failures are rare; instead localized failures on individual ridges or within small regions seem to be more common (Martin 1996). This might explain why during periods of perceived mast failures, we still observe litters with average or above average litter sizes.

Past CABS data indicated that an average of 85% of available females for breeding on the northern and 95% on the southern study were producing cubs (Needham-Echols 2000, Ryan 1997). We observed an average of 55% of all handled females produced cubs each year. The percent varied from 35-74%, but did not show synchronous breeding (i.e., of all or most females producing cubs in alternate years), especially years following a mast failure. We observed 3 of 14 (21%) females producing cubs in consecutive years, 1998 and 1999, following a mast failure in fall 1997. McLaughlin et al. (1994) observed synchronous breeding of black bears in Maine in which 85% of all females produced cubs on even years and 15% produced cubs on odd years, attributing it to a 2-year-cycle of beechnut production.

We observed an unexpectedly high percentage of barren females ranging between 14-29% (of all handled females) per year. Some of these females were expected to have cubs given that they had yearlings the previous winter, but some were newly radio-collared with unknown status. It is possible that some of these barren females were separated from their yearlings after the summer's breeding season. If females lose their offspring before the breeding season, they usually can reach estrus again to breed in consecutive years. McLaughlin et al. (1994) reported 18 of 164 handled females (11%) not reproducing during 1982-1991. Our estimates of barren females are maximum estimates because they include females that we observed in a den but could not access. In some cases it is possible that cubs were hidden under a female and not observed. However, cubs can usually be heard if a den is monitored for 20-30 minutes.

Interbirth interval (1.8 years) seems to be related to complete litter loss and age of sow. Bears in poor nutritional condition may produce cubs, but will lose the litter during denning season due to lack of milk for nursing (M.R. Vaughan, Virginia Polytechnic Institute and State University (VPI & SU), unpublished data). Interbirth interval in Minnesota ranged from 2 to 4 years ($\bar{x}$ = 2.28 years; Rogers 1987); an interval of 4 years was observed following a mast failure of 3 consecutive years. In Tennessee, 8 of 23 females did not reproduce cubs following a poor mast crop production that fall (Eiler et al. 1989). Inexperienced, young bears could be more likely to loose a litter early on and would enter estrus again for the following breeding season, lowering the average interbirth interval for all females. Kolenosky (1990) observed an average interval of 2.7 years between litters, but noted that this value was as low as 2.1 years / litter for older females. In rare instances, researchers have observed an interval of 1 year for bears successfully rearing a litter and producing cubs the following winter (LeCount 1983, Seguin 1992).

Virginia's black bear population does not seem to be limited by reproduction due to average litter sizes (up to 2.35 cubs / year on average), early age of first primiparity (observed reproduction in 2-year-olds), no complete reproductive failure in years of low hard mast production as observed in Maine, and large proportion of reproductively available females reproducing.

Violation of assumptions in the survival analyses

Statistical analyses are tied to assumptions about data that ensure the validity of analyses and estimates. If assumptions are violated, results can be biased or invalid, leading to false conclusions. Survival analysis for population data is a common tool for understanding population dynamics. It is important to be aware of violation of assumptions to evaluate reliability of results.

Radio-collared bears

Most published survival rates for black bears are based on analysis of radio-tracking data. Authors often use the Heisey-Fuller (1985) analysis, which is based on parametric estimation of parameters. One assumption for this analysis is that all individuals within an age and sex class have the same mortality and survival probabilities during an interval (see Methods).

Bear mortality, however, might be related to home range location (Bunnell and Tait 1980). Bears that live closer to roads might be more vulnerable to hunting, road kill or other human-caused mortality. Similarly, bears that live near roads might be more vulnerable to trapping and marking. Kasworm and Their (1994) observed a bias between harvest and trapping method. Like most studies, research – related trapping was conducted within 200m of the road and resulting in marked animals that might be also more prone to harvest. However, since harvest occurs in the same areas (most hunters do not venture far from roads), trapping and hunting could have the same bias. Mortality rates for bears close to roads (the population segment we sampled) may be higher than in remote areas. In our study area, however, there are only a few locations where hunters and researchers do not have access. It might be worth evaluating at the end of CABS if bears in more remote areas have different mortality factors and survival probabilities than in more accessible sections of the study areas.

A second assumption for the Heisey-Fuller (1985) method is that survival an individual animal is independent from another. I believe this assumption is met for our analyses since it was limited to adults or bears already separated from their mothers. This factor might be important when investigating survival of cubs and yearlings dependent on their mothers' survival. The assumption that the sample is representative of the population being studied is probably not met. During our study we had proportions of up to 8.6F:1M radio-collared, with sample size for subadults of only one animal at times (Appendices 2-7). The only precise estimate from this section would be adult females that reached sample sizes of up to 46 animals monitored at one time. In addition, the sample population was not representative for the population as a whole because we did find a significantly higher survival of radio-collared bears than for bears only marked with ear tags.

The Kaplan-Meier survival estimator has similar assumptions than mentioned above and specifically mentions that newly tagged animals have to have the same survival probabilities as previously marked ones (Pollock 1982).

In general, I think that the violations of the assumptions for both survival estimates of radio-collared bears in this study are serious and probably caused the different estimates compared to survival analyses from the ear-tagged population.

Ear-tagged bears

Due to the larger sample size of ear-tagged bears compared to the radio-collared population, assumptions are met better. First, the tagged population is probably close to the population structure of the actual population, especially over time since animals are added to the tagged population every year. By the end of 1999, CABS had marked 746 different black bears on its northern study area (see results). The population segments that are missing in the captures are cubs and yearlings; however, since these age groups were not included in the analyses, they should not bias the results.

An important assumption in mark-recapture studies is that marks are not lost, misread or overlooked. Since we mark bears several different ways (e.g., ear tags, lip tattoos, and radio-collars), the chance of detecting one of the marks is high. We observed < 10 cases of bears losing their ear-tags completely. In some instances one tag is lost, but usually the second one is retained. Proper recording of ear-tag numbers at the check stations was safeguarded by providing a reward for submitting the actual ear-tag to us. Hunters were paid $25 when they returned an ear-tag to us. Questionable observations (e.g. an ear tag was reported from a check station yet the animal was captured in following years) were discarded (N=4). We believe that this assumption was reasonably met.

Mark-recapture studies require equal catchability among individuals (Lebreton et al. 1992). By dividing our sample into age and sex classes, we addressed the heterogeneity of behavior due to age and difference in behavior between sexes. However, there remains a possibility that individuals within these age and sex classes had different probabilities of capture / harvest depending on their home range location. We believe that this effect is not as severe as in the radio-collared sample, yet present. We trapped and marked bears in areas that were accessible only by all terrain vehicles (ATV) and were closed to the public for hunting. Bias can exist for bears that had home ranges not overlapping any roads or trails upon which we trapped. There were 2 wilderness areas (approximately 100 km^2 each) in our study area that were not accessible by vehicle. A few individuals (especially females) that live at the center of these areas may not have had home ranges overlapping with any of the trails we trapped and therefore had low probability of capture. If heterogeneity of capture played a role in our study (i.e., we are capturing animals closer to roads more often than animals more distant), survival estimates could be biased low if bears near roads have lower survival probabilities (Lancia et al. 1994). Since all 3 estimates resulted in similar estimates these biases could have influenced the estimates in similar ways.

I would have expected that the CJS estimate based on summer captures only would be biased more than any other estimates because marking and recapturing methods were the same and would encourage trap-happiness or shyness to show an effect. Since dead returns are a factor in the other 2 estimates, behavioral differences during capture are not relevant.

An assumption for the dead return estimate is that the reporting rate of dead animals is constant across time. I believe we met this assumption because mandatory tooth submissions and harvest regulation have not change during the time of the study. If our data included part of the harvest reports before checking a bear was mandatory, I would be hesitant about this assumption. In general, I believe we met the assumptions for estimators concerning the ear-tagged population better than for the radio-collared sample and gained more reliable estimates from them.

Survival Rates and Mortality Factors

Radio-collared bears

Annual survival estimates for radio-collared adult and subadult female (0.993 and 0.997 respectively) bears were higher than survival rates reported in other hunted bear populations, yet similar to unexploited populations (Table 16). Survival of adult female

Table 16. Annual survival rates for black bears in North America.

State / Province	Status	Adult		Subadult		Estimator	Citation
		Female	Male	Female	Male		
Virginia	Hunted	0.84	0.72	0.72	0.51	Brownie Dead Recoveries	This study
Virginia	Hunted	0.87	0.65	0.80	0.52	Burnham's combined model	This study
Minnesota	Hunted	0.81	0.73	-	-	Cormack - Jolly - Seber	Rogers 1977
Virginia	Hunted	0.84	0.62	0.82	0.46	Cormack - Jolly - Seber	This study
Massachusetts	Hunted	-	-	0.88	0.25	Direct observation	Elowe and Dodge 1989
Ontario	Hunted	0.88	0.77	-	-	Direct recoveries	Kolenosky 1986
Maine	Hunted	0.80	-	0.75	-	Heisey-Fuller	McLaughlin 1998
Virginia	Hunted	0.87	0.61	0.87	1.00	Heisey-Fuller	Hellgren 1988
Virginia	Hunted	0.92	0.73	0.96	0.46	Heisey-Fuller	This study
Virginia	Hunted	0.98	0.90	0.99	0.80	Kaplan-Meier	This study
Alaska	Hunted	0.85	0.72	0.75	0.55	Kaplan-Meier	Schwartz and Franzmann 1991
Montana	Hunted	0.79	0.73	-	-	Kaplan-Meier	Kasworm and Their 1994
Arkansas	Not hunted	0.98	0.85	0.98	0.85	Heisey-Fuller	Clark and Smith 1994
Colorado	Not hunted	0.96	0.70	0.94	0.76	Heisey-Fuller	Beck 1991
Virginia	Not hunted	0.90	0.50	-	-	Heisey-Fuller	Kasbohm 1994
Virginia	Not hunted	0.92	0.59	-	-	Heisey-Fuller	Carney 1985

black bears in hunted populations in North America ranged between 79-88% (Table 16), 61-77% for adult males, 75-88% for subadult females, and 25-100% for subadult males.

Since we found a significant difference in survival rates of radio-collared versus non-radio-collared females (adults and 3-year-olds), we suspect that hunters avoided harvesting radio-collared bears. The harvest rate of radio-collared adult bears (weighted mean: M: 0.13, S.E. 0.04; F: 0.06, S.E. 0.02; Fig. 4) was lower than the harvest rate for ear-tagged adult bears (M: 0.19 S.E. 0.06; F: 0.13, S.E. 0.07; Table 15). Many hunters knew from conversations with CABS personnel that we collared mainly females (Appendix 2). This fact has changed little except in 1998 when the proportion of radio-collared females was 1M:2.6F (Appendix 2). The low proportion of radio-collared males harvested compared to males marked with ear-tags only shows that selective harvest by hunters might have increased survival estimates across all age and sex classes for the radio-collared sample.

Survival estimates (both Heisey – Fuller and Kaplan – Meier) for radio-collared adult and subadult males exhibited broad confidence intervals (Table 13, Appendices 3 and 5) due to small sample sizes. We did not find a radio-collar effect for 2-year-old females and males, probably also due to small sample sizes. In addition, the effect was only detected for the dead recovery analysis. Since the other 2 analyses included summer captures, during which we also captured radio-collared bears, the radio-effect should be less apparent in comparison.

Survival rates in all models (Heisey – Fuller and Kaplan – Meier) were constant across years except for subadult males. The difference in annual survival rates for subadult males is probably related to small sample size. We monitored only 1 to 7 subadult males at any given time because we lacked a safe expandable collar for this fast-growing age-class (Appendix 3). Survival rates for adult males in 1994 and 1995 should be viewed with caution since they are based on sample sizes of 4 and 6, respectively (Appendix 5). The development and use of ear tag transmitters since 1999 should provide better estimates of survival for subadult black bears in Virginia by the end of this study.

Black bear harvest increased from 115 animals harvested in 1994 (in Rockingham and Augusta counties combined) to 235 animals harvested in 2000 (VDGIF, unpublished data). One might expect survival rates to decrease across years with increasing harvest numbers. However, the estimated survival rates did not reflect this trend, Virginia's black bear population must be increasing if survival rates stayed the same yet harvest numbers increased. For example, if mortality rate (in this case assumed to equal harvest rate) stayed 20% across years, the population must have risen from 575 in 1995 (115 animals harvest = 20% of 575) to 1,175 animals in 1999 (235 animals harvested) to sustain a 20% mortality and not decline, indicating population growth over the last 5 years (for more detail on this see Chapter 5).

Information on natural mortality of bears is scarce (Hellgren 1988, Rogers 1987). Kolenosky (1986) calculated 10-15% natural mortality for adult bears in Ontario and 17-38% natural mortality for subadults by dividing the number of tagged bears never recovered by the total number of different bears tagged (Jonkel and Cowan 1971). In our study, 15% of all mortalities was either natural or of unknown cause. Many studies are short term, and bears lose their collars and are replaced by new animals with a new chance of natural mortality. Large long-term studies have been conducted in Great Smoky National Park (GSNP(Pelton and Van Manen 1996), northern Maine (McLaughlin 1998), and this one. Pelton and van Manen (1996) pointed out that long-term studies can produce different results than short-term studies. They interpreted population data from black bears in GSNP and came to different conclusions using a 5-year, 10-year, and 28-year dataset. However, the authors indicate that funding for such long-term studies is difficult to maintain.

Surprisingly, few studies use capture-recapture data to estimate survival. Most of the necessary data are collected to conduct such analyses, but the analyses are lacking. Since we found such a discrepancy between survival of radio-collared and non-collared bears, it might be valuable for future bear studies in hunted areas to consider how collaring animals might bias the data derived from the collared bears. I would caution against the use of survival estimates from the telemetry analyses of these data, and would recommend the use of survival estimates from the mark-recapture data for Virginia's black bear population (see below).

Ear-tagged bears

Survival rates calculated from ear-tagged black bears in Virginia were similar to rates reported for other hunted populations in North America (Table 16). Survival rates for subadults are rarely reported due to difficulties in monitoring dispersing animals (Beck 1991, Rogers 1976a). In this study, survival rates for subadult black bears {2-year-old males: 0.335 (Dead recoveries) - 0.461 (CJS); 2-year-old females: 0.530 (CJS) - 0.812 (Burnham's combined; Table 14)} were lower than for adult black bears {(males: 0.620 (CJS) - 0.769 (Dead recoveries); females: 0.812 (Burnham's combined) - 0.840 (dead recoveries)}, with subadult males (2 and 3 years old) experiencing the lowest survival rate of all age and sex classes. Bunnell and Tait (1985) suggested that subadults suffer higher mortality due to dispersal. Furthermore, intraspecific competition for home ranges might add to a subadult's mortality as we observed in the cannibalism of a 2-year-old male on this study. Greater dispersal distances may make subadult males more vulnerable to mortality (human encounters, starvation, aggressive encounters with other bears, getting killed by vehicle collisions, etc.) than subadult females (Schwartz and Franzmann 1992).

Female survival was highest for all age and sex classes. Virginia's late hunting season (December) may eliminate many females from harvest due to early denning, especially when pregnant (Godfrey 1996). Virginia law, which prohibits the harvest of females accompanied by cubs, also may explain the high survival of females in this study. In addition, as mentioned above, Virginia bear hunters may avoid the harvest of females and increase their survival rates compared to males.

We observed low natural mortality in ear-tagged bears, because we most often could not find dead bears without radio-collars. The few instances that we observed were incidental finds by hunters, game wardens or CABS personnel.

For both ear-tagged and radio-collared bears, hunting was the major cause of mortality (85% of total mortality), mainly affecting subadult males. Bears experience 90% hunting mortality in Minnesota (of total mortality; Rogers 1976a), 83% in Arizona (LeCount 1982), and > 90% in Alaska (Schwartz and Franzmann 1991). In protected areas in Virginia, bears experienced 30-50% hunting mortality (of total mortality), since home ranges often extended beyond park boundaries (Hellgren 1988, Kasbohm 1994). Natural mortality was 12% of the total mortality for the radio-collared sample.

Survival rates for Virginia's hunted black bear populations are similar to other exploited populations in North America (Table 16). I believe the survival estimates of the ear-tagged population are more realistic than the survival analysis on data of the radio-collared population. Monitoring of the radio-collared population, however, can give us insight into natural causes of mortality, which is difficult to obtain from only ear-tagged populations.

The dead recoveries estimate is probably the best of the 3 because it used different methods of capture and recapture (harvest) and excluded the radio-collared bears (due to higher survival for radio-collared bears). It was therefore used in model simulations in Chapter 5.

Virginia black bear harvest, harvest rates, and hunter participation

Bear harvest in Virginia started to increase dramatically after 1980, 6 years after the hunting season was shortened by 2 weeks and moved later into the fall (September). The regulation change resulted in a decrease of average percent females harvested by 8%, from 46.4% (1963-1973) to 38.3% (1974-1998). This may have resulted in higher survival of reproductively active females in the population helping to explain the apparent increase in population size and with it, increased harvests. The fact that bears in Virginia start reproducing at age 3 but do not reach their peak of reproductive output until age 6 (Table 6), might explain the time lag of an increase in total harvest until 1980.

McLaughlin (1998) reported that the female black bear population in Maine that exhibited highest vital rates (e.g., high litter size, no synchronous reproduction, high percent of females breeding) could sustain 15% hunting mortality; populations with alternate-year litter production could sustain 10% annual hunting mortality, and populations with low litter production could sustain 5% mortality without declining. In Virginia, female black bears currently exhibit hunting mortalities of 0-33% / year (weighted mean: 13%). Given McLaughlin's (1998) analysis, Virginia's female black bear population might be able to sustain the current level of harvest and still stay stable or increasing (due to similar cub reproduction, no synchronous breeding and a large percent of available females (85%) breeding as described by McLaughlin 1998).

Subadult males were most vulnerable to harvest in Virginia (75% of total male harvest or 47 % of total harvest; Martin and Steffen 2000), probably due to increased movement during dispersal, larger home ranges and inexperience in avoiding hunters (Bunnell and Tait 1980, Kasworm and Their 1994, Rogers 1976a).

The surprising negative correlation between statewide hunter effort and harvest numbers can be explained in several ways. First, the bear population could have increased, making it easier for hunters to find bears. Second, hunters became more skilled or used better equipments (like telemetry collars to find their dogs) to hunt bears, or third, bears were easier to find because they were attracted to bait stations (which are located near roads) which hunters started using after 1993 when a dog-training season was established (D. Thorn, president Virginia Bear Hunters Association, personal communication). I believe that it is probably a combination of all 3 factors, but generally points to an increasing bear population trend.

CONCLUSIONS

Virginia's hunted bear population had survival rates and hunting mortality similar to other exploited bear populations in North America. Two-year-old males were most affected by harvest with mortality rates averaging 0.45, but reaching as high as 0.65 during 1996 (Table 15). However, adult female survival, which has been reported as most important for population growth (also confirmed for this study in Chapter 5), was 84% (dead return estimate), well within the range of other exploited populations.

The dead return estimate was used for simulations in Chapter 5 because it uses differing methods for marking and recapturing (harvest) and excluded radio-collared bears in the estimation process. Sample sizes of the initial capture were much larger than for radio-collared bears and were more representative of the population as a whole. Additionally, marking bears of all age classes is easier than keeping a radio-collar on an animal. Adult males were much more difficult to keep radio-collared due to their large neck size in relation to their head (they could slip the collar over their head).

Survival estimates derived from radio-collared bears in this study seem to be biased positive and should be discarded in favor of estimates from ear-tagged bears. Bias in the estimates seemed to be related to hunter selectivity against radio-collared bears. However, radio-telemetry in this study is valuable for estimating of natural mortality, an estimate commonly lacking in the literature, and estimating reproduction.

One question, however, is how important accurate survival estimates are for males? Female survival seems to drive population growth (Chapter 5) and males do not seem to be limited since most available females are bred every year. However, studies on changes in breeding success of subadult males in heavily exploited populations might be a worthy endeavor. By harvesting large trophy males and keeping the male population at very low levels, we may encourage the breeding by males that are not as 'fit' genetically as more experienced males. Theses studies would entail genetic analysis of percent of offspring fathered by a large male in a particular area and proportion of offspring fathered by the same individual over its home range.

CHAPTER 2. POPULATION ESTIMATION

Studies on ecology of Virginia's hunted black bear population mostly have been limited to information from nuisance bears since 1957 (Strickley 1961). Little information on population size, reproductive and survival rates, non-hunting mortalities, and denning ecology has been available to aid management of the hunted population. The types of data needed for management of wildlife is often debated in the scientific literature. Agencies need reliable data concerning population demography or, at least population trends for management. Researchers argue how detailed data should be as an effective management tool (Roseberry and Woolf 1991). Hayne (1984), for example, argued that it is often sufficient to know only a population's position in relation to carrying capacity and whether or not the population is increasing or decreasing.

Estimation of population size has been approached from many different angles. The earliest approaches were developed by Petersen (1896), followed by Lincoln (1930), who applied mark-recapture data and assumed geographic and demographic closure. They estimated population size with $\hat{N} = \frac{n_1 * n_2}{m_2}$, where n_1 is the number of marked animals in the population, n_2 is the number of animals recaptured on occasion 2, and m_2 is the number of marked animals recaptured on occasion 2 (commonly known as a Lincoln-Petersen estimate). Chapman (1951) developed an unbiased estimator based on the original Lincoln-Peterson equation: $\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$.

Additional model have been developed for removal estimators (Zippin 1956) and multiple recapture occasions (Schnabel 1938). Overviews of available estimators, study design, and assumptions are summarized by Otis et al. (1978), White et al. (1982), and Seber (1982).

An important assumption of closed population estimates such as Lincoln-Petersen or Chapman's modification is demographic and geographic closure (White et al. 1982). The closure assumption is critical in that it assumes a fixed population size *N*, which can be estimated during the mark-recapture period. Demographic closure (i.e., no births or deaths) is usually achieved by conducting the study outside the season of births and keeping the sampling period short to reduce the likelihood of deaths; game animal studies are usually conducted outside the hunting season to ensure that there are no harvest-related deaths. Geographic closure (i.e., no immigration or emigration) can be evaluated from the movements of radio-collared animals in and out of the study area. Studies should be conducted during periods when minimal movement of the animal is expected, such as when soft mast is available to keep bears in a small area. If geographic closure is violated and marked animals are leaving the population, population estimates for an area are biased high since more animals are estimated to live in an area than actually do.

When animals do leave the study area, the effective area A is greater than the study area A* (White and Shenk, unpublished manuscript). Radio-collared animals can provide an estimate of the proportion of time an animal spends on a study area (see methods below). If the population experiences death, permanent migration (in or out of the study area), and recruitment, an open population estimate such as the Jolly-Seber estimate might be more appropriate (Seber 1986). These models are equipped to deal with permanent but not temporary migration, which might be interpreted has capture heterogeneity (Seber 1986). When recapture rates in successive sampling periods are low, population estimates might not be valid due to large confidence intervals. Low recapture rates for Virginia's black bear population between years are possible due to high harvest numbers in the study area, emigration from the area and differing trapping routes among years.

The goal of this chapter is to estimate population size on the CABS northern study area. We used several approaches to population estimation using the same data to observe variability in estimates, evaluate the impact of violation of assumption on estimation, and provide density estimates for Virginia's hunted black bear population.

METHODS

For general capture techniques see General Methods section (pages 13-15).

Camera Study Setup

Forty-eight to 50 cameras, including 15-27 passive infrared-triggered cameras (Camtracker, Athens Georgia), and 33 manual cameras built by CABS (Martorello et al. 2001), were distributed in a grid system of 1 camera / 2-km^2-grid cell on a sub-study area of 100 km^2. The area was located in the center of the northern study area between Rt. 33 and Briery Branch Road.

The 2-km^{2}grid size was smaller than the minimum home range size of black bears within the study area (Higgins 1997*a*). Thus, each bear residing within the sampling area should have been available for sampling. The camera sites were baited every 3 days and checked for function and film status.

Bears captured within this sub-area during the summer capture season were marked with tri-colored ear streamers that were attached to the perma-flex ear tags (see page 14) each captured bear received on the study area as a whole. Each individual bear received a unique color code, e.g. ID#1: dark blue, red, white, ID#2: green, yellow, orange. The streamers were 1.3 x 23 cm strips and consisted of rubber-coated vinyl. They were attached to the ear tags by inserting them into a whole in the ear tag and fastening them with a zip-tie (Martorello et al. 2001).

The first sampling period was conducted from mid August to early September when hound-training season started, ranging between 14-17 days (Table 17). The second period lasted from the beginning of October (after the hound training season) to the 3rd week in October (21 to 30 days, Table 17). To improve the demographic closure assumption, we chose a 2-week and 4- week sampling period during the summer and fall, respectively, when mortality is low, bears do not move very much within their home ranges and the period between mark and resight occasions was short.

Data Analysis

Mark-recapture analysis using summer captures

We used several approaches to estimate population size of Virginia's hunted black bear population. Estimates were based on mark-recapture data from summer trapping seasons 1994-2000. First, we used Chapman's (1951) modification of the Lincoln-Petersen estimate for single mark-recapture events, with the estimate $\hat{N} = \frac{(n_1+1)(n_2+1)}{(m_2+1)} - 1$, where n_1 is the number of marked animals in the population, n_2 is the number of animals recaptured on occasion 2, and m_2 is the number of marked animals recaptured on occasion 2. Its variance is $\hat{\text{var}}(\hat{N}) = \frac{(n_1+1)(n_2+1)(n_1-m_2)(n_2-m_2)}{(m_2+1)^2(m_2+2)}$. We constructed 1 estimate for each of the 6 summers, dividing a summer into a marking period and a recapture period. The marking period extended through the first half of the total time trapping occurred, the recapture period being the latter half of the period. Marked bears that died between sampling periods due to handling or other causes were removed from the sample. This estimate assumed population closure, which was relaxed by assuming equal probability of loss between marked and unmarked bears (Seber 1982). The assumption of equal probability of capture was not met for different age and sex classes (see Chapter 1). Other assumptions, including marks are not lost, are thought to be met.

Secondly, we used the Jolly-Seber estimate of program MARK to obtain an open population estimate (White 1993). We treated each summer trapping season as an individual trapping interval and ignored recaptures within an interval.

Mark-recapture analysis using recovered ear tags during the harvest season

Hunters in Virginia are required to check harvested bears at VDGIF check stations. The ear tag and tattoo numbers of marked bears that were harvested were recorded and provided to CABS (VDGIF pays a $25 reward for returned ear tags and CABS paid a $50 reward for retuned radio transmitters). I analyzed harvest data with the modified Chapman (1951) estimate (see above) treating returned ear tags of the harvest season and other reported mortalities (e.g., natural, road kills, nuisance) within the 2 counties of the study area (Rockingham and Augusta) as my recapture sample. I used reported counties for identifying the 'recapture' sample, because harvest check cards only identify the county that a bear was harvested in and not the specific location within that county. Marked animals from the previous summer trapping produced the marked sample.

Mark-recapture analysis using tetracycline markers

Each captured bear was injected with a tetracycline marker (see Trapping and Handling Method) that could be identified in cementum annuli of returned teeth from the winter bear harvest (VDGIF requires hunters to submit a tooth from each harvested bear). Teeth were analyzed by Matson's Laboratories (Missoula, MT) to identify when and how many times a bear was marked with tetracycline. This mark has the benefit that it cannot be lost by an individual. However, Garshelis (1991) noted that this method only detected 85-90% of tetracycline marks administered to bears.

We used the modified Chapman (1951) estimate for population size, using tetracycline marked teeth as our recapture sample. The time interval between marking and recapture ran from summer (when trapped bears were handled and marked) to fall harvest. Ideally, this estimate should be identical to the harvest return estimate from ear tags described above, and was used to check the accuracy of the marking technique with tetracycline.

Mark-resight analysis using camera survey

The 6 data sets (2 estimates each for 1998-2000) were analyzed in the NOREMARK program for the Bowden's estimator (White 1996). The assumptions included; 1) population closure (demographic and geographic), 2) marks were not lost between sampling periods, 3) marked individuals were a random sample of the population, and 4) sighting is independent of mark status (e.g., marked and unmarked animals have the same sightability). Minta and Mangel (1989) proposed a bootstrap estimate of population size projected from sighting frequencies of individual marked animals. For the unmarked population, sighting frequencies are drawn randomly from the pool of observed sighting frequencies. Bowden (1993) extended the estimate by using confidence intervals based on the variance of the resighting frequencies for the marked population.

The loss of marks was investigated by visiting radio-collared animals in the winter dens and determining percent loss of ear streamers. We recognize that streamers could be lost between the end of the camera session and the den season (especially from the August session), which would make the loss rate higher than it was during the camera sessions.

Mark-recapture analysis using hound chase season data

Virginia's September bear-hound training season began immediately following the summer trapping season (June through August) and continued for 5 weeks. During the season, bears can be chased by bear hunters, but must be released if treed by hounds. We accompanied bear hunters on these chases to determine if the treed bear was marked or unmarked. Starting in 1998, we also provided bear hunters in the study areas with diaries to note how many bears they tree and if CABS marks were present. These data then were treated as mark-recapture data. Since the marking event of the summer and the "recapture" event of a treed bear occur back-to-back, we assumed population closure for the Lincoln-Petersen estimate was met.

Correction factor for violation of closure assumption

When estimating density, they study area on which trapping is conducted is assumed closed, so that density $\hat{D} = \frac{\hat{N}}{A}$, where $\hat{N}$ is the estimated population size and A is the size of the study area. Animals that live at the edge of the trapping grid pose a problem to defining the size of A since they might spend part of the time outside the trapping area. Nested grids and buffer strips around the area have been used to remove this problem (Otis et al. 1978, White et al. 1982, Garshelis 1991).

Radio-marked animals provide another alternative to correcting density estimates (White and Shenk, unpublished manuscript). Animals radio-marked within the trapping grid can be monitored for the proportion of time they spend on the area. The probability of an animal to be on the study area was calculated as $p_i = {g_i}/{G_i}$, where g is the number of locations for a radio-collared animal on the study area, and G the total number of locations of an animal. The mean proportion ($\overline{p}$) and its variance [var ($\overline{p}$)] were applied to correct population size $\hat{N}$ and its variance, which could reduce $\hat{N}$ if bears spend a significant amount of time outside the study area. Thus, $\hat{D} = \frac{\hat{N} * \overline{p}}{A}$, where D is density and A is study area size, and $\mathrm{var}(\hat{D}) = \frac{[\hat{N}^2 * \mathrm{var}(\overline{p})] + [\overline{p}^2 * \mathrm{var}(\hat{N})]}{A^2}$ (White and Shenk, unpublished manuscript).

RESULTS

Site fidelity of radio-collared bears on the camera area

We monitored between 3 and 18 adult females and 1 to 5 adult males during June to November 1997-2000 on the camera area (see above) to evaluate the closure assumption required in many population estimates. On average, females were located on the study area 86 % ± S.E. 2 of the time, and males were located on the study area 70% ± S.E. 10 of the time (Table 17). During August (first session of the camera study) of all 3 years, bears spent 71 % ± S.E. 8 (1998) to 85 % ± S.E. 10 (1999; available for females only) of the time monitored on the study area. In October (second session of the camera study), locations on the study area ranged from 76 % ± S.E. 8 (1998) to 86 % ± S.E. 11 (2000).

Population estimate using summer captures

During summers 1994-2000 we trapped 538 individual bears 1,008 times (Table 18). Using the Lincoln-Petersen estimate with Chapman’s modification, black bear population estimates for the camera area ranged from 87 – 92 animals during 1998 – 2000 (Table 19). When adjusted for the proportion of observations radio-collared bears

Table 17. Proportion of observations (reported as means) radio-collared bears spent on the camera study area on the northwest study area of the Cooperative Alleghany Bear Study for 1998 – 2000 on the George Washington and Jefferson National Forests, Virginia.

Month/Year	Male	S.E.	*n*	Female	S.E.	*n*	Both Sexes	S.E.
Jun-98			0	0.94	0.06	8		
Jul-98			0	1.00	0.00	3		
Aug-98	0.43	0.23	3	0.78	0.08	12	0.71	0.08
Sep-98	1.00		1	0.87	0.09	9		
Oct-98	0.70		1	0.76	0.08	13	0.76	0.08
Nov-98			0	1.00	0.00	10		
1998	0.60	0.17		0.86	0.03		0.84	0.03
Jun-99			0	1.00	0.00	5		
Jul-99	1.00		1	1.00	0.00	4		
Aug-99			0	0.85	0.10	8		
Sep-99			0	1.00	0.00	5		
Oct-99	0.73	0.27	3	0.81	0.07	18	0.86	0.07
Nov-99	1.00		1	0.93	0.07	11		
1999	0.84	0.16		0.90	0.03		0.89	0.03
Jun-00	1.00		1	1.00	0.00	4		
Jul-00	1.00		1	0.73	0.13	9		
Aug-00	1.00		1	0.80	0.13	8	0.82	0.12
Sep-00	1.00		1	0.81	0.11	7		
Oct-00	0.00		1	0.83	0.13	6	0.86	0.11
Nov-00	0.00		1	0.81	0.10	8		
2000	0.66	0.21		0.81	0.05		0.79	0.05
Total	0.70	0.10		0.86	0.02			

Table 18. Trapping summary for the northwest study area of the Cooperative Alleghany Bear Study for the summers 1994 – 2000 on the George Washington and Jefferson National Forests, Virginia.

	Summer 1994	Summer 1995	Summer 1996	Summer 1997	Summer 1998	Summer 1999	Summer 2000	Totals
Original Captures								
Males	76	52	39	42	44	56	32	341
Females	35	29	25	34	28	29	17	197
Subtotal	111	81	64	76	72	85	49	538
Recaptures [a]								
Males	21	27	44	39	46	47	37	261
Females	2	14	30	42	31	42	48	209
Subtotal	23	41	74	81	77	89	85	470
Totals	134	122	138	157	149	174	134	1,008

[a] recapture include animals that were caught in previous trapping years

Table 19. Population estimates (of bears > 17 months) using a Lincoln-Petersen estimate with Chapman's (1951) modification on the camera study area (100 km^2) of the northwest study area of the Cooperative Alleghany Bear Study for the summers 1998 – 2000 on the George Washington and Jefferson National Forests, Virginia.

Sex	Year	# Marked bears [a]	# Marked bears recaptured [b]	# Unmarked bears captured	Population Estimate ($\hat{N}$)	95% C.I. ±	$\overline{p}$ [c]	Adjusted Population Estimate ($\hat{N} * \overline{p}$)	Density / km^2	95% C.I. ±
Both	1998	29	11	23	87	57-117	0.84	73	0.73	0.51
Both	1999	34	12	19	85	57-113	0.89	76	0.76	0.49
Both	2000	31	10	21	92	57-127	0.79	73	0.73	0.68
M	1998	17	8	8	33	23-43	0.60	20	0.20	0.26
M	1999	18	9	7	31	23-39	0.84	26	0.26	0.23
M	2000	16	7	13	44	27-61	0.66	29	0.29	0.46
F	1998	12	3	15	61	21-101	0.86	52	0.52	0.45
F	1999	16	3	12	67	22-113	0.90	60	0.60	0.52
F	2000	15	3	8	47	17-77	0.81	38	0.38	0.38

[a] Time period of marking: 1998: June 6 - July 8; 1999: June 6 - July 15; 2000: May 16 - July 25

[b] Time period of recapture: 1998: July 9 - August 8; 1999: July 16 - August 24; 2000: July 26 - August 23

[c] average proportion of occasions bears were located on the study area (100 km^2; Table 13)

were located on the study area (used average annual estimates; Table 17), population estimates fell to 73 – 76 bears or 0.73 – 0.76 bears / km^2.

I attempted to estimate population size the same way for the entire study area, but was unsuccessful due to lack of recaptures within large portions of the area during the summer months, especially for females (Appendix 7). Population estimates with low recapture rates resulted in low population estimates that are probably not valid (Appendix 7). Open population estimates (Jolly-Seber) attempted with program MARK, could not be rendered due to even lower recapture rates and had to be abandoned.

Population estimate using recovered ear tags during the harvest season

Using the Lincoln-Petersen estimate with Chapman's (1951) modification, black bear population estimates for the northern study area ranged from 582 – 1,026 animals during 1994 – 1999 on the 860 km^2 area (Table 20), with population densities ranging from 0.68 – 1.19 bears / km^2.

In 1998, hunters took a record 28 of 101 marked bears, resulting in a harvest rate of 28% (Table 20). For females, record harvest rates were observed in 1994 (21%), 1997 (16%), and 1998 (15%).

Population estimate using tetracycline markers

Population estimates using tetracycline markers from teeth turned in during the harvest did not show similar estimates to the harvest tag return estimates. For example, 20 (12M:8F) of 135 bears marked with tetracycline during 1997 were harvested, but only 7 (6M:1F) were detected during the analysis by Matson's laboratory (see Methods). This resulted in a detection rate of 35%. When using these numbers in a Lincoln-Petersen estimate, we generated population estimates of 4,410 (95% C.I.: 1,193-7,627) bears for the northern study area. This is up to 10 times the estimate from above.

Detection rates in 1998 were better; 42 (29M:13F) of 148 marked with LA 200 were harvested, and only 32 (24M:8F) were detected by tetracycline analysis, resulting in a detection rate of 76%. Due to the unreliable detection rate we did not proceed with further population estimates using these data, but have returned the teeth for re-analysis to Matson's Laboratory.

Table 20. Population estimates (bears > 17 months old) using a Lincoln-Peterson Estimate with Chapman's modification on the northern study area (860 km^2) of the Cooperative Alleghany Bear Study for the summers 1994 – 1999 on the George Washington and Jefferson National Forests, Virginia, using harvest returns as the recapture event.

Sex	Year	# Marked bears	# Marked bears harvested	# Unmarked bears harvested	Harvest rate	Population Estimate ($\hat{N}$)	95% C.I.	Density / km^2
Both	1994	91	18	130	0.20	720	456-984	0.84
Both	1995	75	17	130	0.23	624	397-855	0.73
Both	1996	85	17	104	0.20	582	366-798	0.68
Both	1997	102	21	190	0.21	992	651-1,333	1.15
Both	1998	101	28	147	0.28	618	509-790	0.72
Both	1999	111	23	196	0.21	1,026	688-1,364	1.19
M	1994	62	12	81	0.19	455	257-653	0.53
M	1995	42	15	101	0.36	313	203-423	0.36
M	1996	42	16	73	0.38	227	153-301	0.26
M	1997	46	12	122	0.26	487	280-694	0.57
M	1998	53	21	98	0.40	294	210-378	0.34
M	1999	58	20	145	0.34	465	318-513	0.54
F	1994	29	6	49	0.21	239	102-276	0.28
F	1995	33	2	29	0.06	362	38-688	0.42
F	1996	43	1	31	0.02	725	0-1505	0.84
F	1997	56	9	68	0.16	444	221-667	0.52
F	1998	48	7	49	0.15	348	154-542	0.40
F	1999	53	3	51	0.06	742	137-1,347	0.86

Population estimate from camera study

During the summer of 1998, 1999, and 2000 we conducted 6 camera surveys. We marked 54 bears with ear tag streamers during summer 1998, 49 bears in 1999, and 47 in 2000. Population estimates during 1998-2000 ranged between 91-131 in August and 83-112 in October (Table 21). The number of individuals that constituted the resighted bears ranged from 12 – 29 individuals. One female in 1999 was resighted 15 times during the 2-week period in August and had a large influence on heterogeneity of resight probability in the estimate. When corrected for proportion of occasions bears were located on the study area, population estimates during those 3 years ranged from 63 to 96 bears (Table 21). During all sessions we photographed a large number (45-122) of non-target species (deer, raccoon, flying squirrel, spotted skunk, people), especially on sites close to water or trails.

Fall sessions were 2 weeks longer than summer sessions to obtain a minimum of 50% resight rate of marked bears. In 1998, we stopped before reaching our goal due to the start of deer hunting season. We did not want any cameras on the study area due to increase chance of theft with increasing numbers of hunters on the study area. Each year between 1-3 cameras (and their film) were stolen even though they were secured with locked cables around trees.

Population estimate using hound chase season data

Unfortunately, we did not obtain enough reliable data from the bear-dog training season to use for population estimation. The selection of hunters we accompanied during the chase season was not random. There were only 10 different groups of hunter on the northern study area who were willing to be accompanied by CABS personnel and volunteers. The area these groups covered did not encompass the entire study area and was focused on areas with high road accessibility and high density of feeding sites. In 1998, we provided hunters with a diary to fill out when we could not accompany them on their chases, but only received 4 replies out of 58 mailed surveys (7% response rate). In 1999, we tried to fill out surveys by calling hunters at the end of each week to ask about treeing success, but received unreliable answers for marked bears (e.g., hunters would

Table 21. Population estimates (bears > 17 months old) using Bowden's estimate on the camera area (100 km^2) of the northwest study area of the Cooperative Alleghany Bear Study for the summers 1998 – 2000 on the George Washington and Jefferson National Forests, Virginia.

Study period	# Marked bears	# Marked bears resighted	# Marked individuals resighted	# Unmarked bears observed	Population Estimate ($\hat{N}$)	95% C.I.	$\overline{p}$ [a]	Adjusted population estimate ($\hat{N} * \overline{p}$)	95% C.I.	Density / km^2
Aug 30 – Sep 14, 1998	50	42	17	86	131	89-191	0.71	93	63-136	0.93
Aug 19 – Sep 5, 1999	42	54	29	71	92	61-141	[b] 0.85	78	52-120	0.78
Aug 6 – Aug 20, 2000	44	91	25	107	91	68-120	0.82	75	56-98	0.75
Oct 1 – Oct 28, 1998	54	23	12	13	83	59-117	0.76	63	45-89	0.63
Oct 5 – Oct 27, 1999	42	37	14	58	99	67-145	0.86	85	58-125	0.85
Oct 1 – Oct 24, 2000	45	39	18	83	112	73-173	0.86	96	63-145	0.96

[a] average proportion of occasions bears were located on the study area (100 km^2; Table 13)

[b] based on females only because no male was radio-collared during this time

identify tag colors for treed bears that we did not use in the study). Due to this unreliable information we abandoned this population estimate.

DISCUSSION

Researchers argue about the value of population estimates for effective population management (Hayne 1984, McCullough 1979). Constituents of wildlife management agencies often inquire about population abundance, and managers themselves are often concerned about animal abundance in their conservation efforts (Garshelis and Visser 1997, Mowat and Strobeck 2000). Reliable estimates are difficult to obtain, however, and involve intensive sampling efforts (Garshelis 1992, McLellan 1989, Miller et al. 1997).

Estimating black bear population density is complicated by low bear densities, inaccessible habitat, lack of vocalization, capture difficulties, ability of bears to move great distance in a short period of time, and lack of adequate estimation techniques (Godfrey 1996, Miller et al. 1987, Pelton and Marcum 1977). Direct counts are only applicable in areas with open terrain and not useful in areas outside the northern tundra (Miller et al. 1987, Pelton 1982). Kane and Litavaitis (1992) showed that behavioral differences between male and female bears can bias capture and harvest data. Male bears are more likely to be harvested or captured due to larger home range sizes. In case of heterogeneity of capture or harvest data, the frequently used Jolly-Seber estimator is negatively biased for population size and survival (Pollock 1982). Biases have also been found in the Lincoln-Peterson estimate due to violation of the equal catchability and observability assumption (Bartmann et al. 1987, McCullough and Hirth 1988). I used the Lincoln-Petersen estimate instead of more complex models that incorporate heterogeneity (Otis et al. 1978, White and Burnham 1995), because the heterogeneity models perform poorly (are less accurate) than the simple Lincoln-Petersen estimate if sample sizes are low or certain sex and age groups are underrepresented (Menkens and Anderson 1988). Moreover, these models require individual capture histories, which are not available for all data types we have. In fact, they would only be available for our summer capture since harvested bears cannot be recaptured several times.

Accurate population estimation for this species is also complicated by hunter selection and varying vulnerability to capture and harvest due to different home range sizes. Several problems existed for obtaining reliable estimates of population size for Virginia's hunted black bear population.

Closure assumption violation

Demographic and geographic closure is an important assumption for using closed population estimates such as Lincoln-Petersen estimates (Pollock et al. 1990, White et al. 1982). Radio-collared males and females spent an average of 84 ± 2 % of all observations on the camera study area of the northern study area of CABS during 1998-2000. We adjusted calculated population estimates for the camera area (Garshelis 1991). The observed variation between sexes ($t = 2.195$, $df = 163$, $P = 0.03$) can be attributed to a combination of the behavioral difference between sexes (males have larger home ranges), individuals collared during that time and the variation of sample size monitored among years. Most of the time, we had only 1 male radio-collared on the camera area. Others passed through but were not collared on the area and were therefore not included in the sample (White and Shenk, unpublished manuscript). This is a serious violation of the closure assumption and should be investigated further, especially for males (increase their sample size in monitoring).

Several other approaches have been used to deal with edge-effects of study areas, including the commonly used buffer strip of ½ of the diameter of the average home range (Dice 1941), using nested trapping grids (Otis et al. 1978, Wilson and Anderson 1985), and by using a boundary strip that encompasses the distance between trapping sites for subsequent captures (Johnson et al. 1987). Most of these, however, have been developed for small mammal or bird studies with animals of smaller home ranges. In our case, there was considerable variation in the number of observations on the area over the course of the year (Table 17).

A second method of investigating violation of closure is to look at the number of marked bears that were harvested outside the study area. In the 6 years of the study, only 5 bears were checked at check stations outside the 2 counties they were marked in; 1 male in 1997, and 3 males and 1 female in 1998. We therefore assumed the closure assumption met for the entire study area and did not correct the population estimate. One has to keep in mind, however, that harvest information only indicates where the bear was checked, not where it was harvested and one has to assume that the bear was checked in the county it was harvested. During the hunting season (December / January) I expected high fidelity to the study area since bears were preparing to den and did not move very much (CABS, unpublished telemetry data).

The more serious violation of demographic closure (no births, deaths or permanent immigration or emigration) does not apply in our case because sampling took place outside of the birth season (January) and harvest season (December / January). A point that is often forgotten is that open population models (e.g., Jolly Seber) were developed to handle violations of this kind of closure, but not violation of geographic closure (i.e. temporary emigration and immigration), a problem more commonly encountered (White et al. 1982).

Violation of equal catchability assumption

Recapture rates outside the camera area were 28% for adult females versus 44% for adult males (Table 14). Lower recapture rates for females resulted in higher variance in their population estimates reflected in larger confidence intervals (Seber 1986). Population estimates using both male and female data in one estimate should be treated cautiously and might not be statistically valid (Otis et al. 1978).

Reliable estimates for population abundance can be achieved if > 45% of the total population has been marked (Bartmann et al. 1987). In this study, 34-40% of the population on the camera area may have been marked, based on, for example, 34 marked animals in 1999 yielded an estimate of 84 individuals with Chapman's modified LP estimate (Table 19). Using Bowden's estimate, 39-65% of the whole population was marked (e.g., in August 2000: $\frac{44 marked}{70 population estimate} = 0.63$; Table 21). When looking at the entire study area, however, only 11-19% of the whole population was marked (based on estimates from harvest return estimates, Table 20).

Population estimate using summer captures

Estimation of population size using summer captures proved difficult except for the camera area, in which we had intensive trapping efforts resulting in high recapture rates and marking of a large portion of the entire population. However, Otis et al. (1978) and (White et al. 1982) cautioned that estimates from experiments in which only 10-20 animals were marked and behavioral responses (such as trap happy or shy) and/or capture heterogeneity are present, estimates might be unreliable. This is the case for this study if males and females are treated separately, as they should be due to heterogeneity of capture probability. Population estimates from the camera area using Lincoln-Petersen's estimator indicated a population density of 0.73 – 0.76 bears / km^2 (Table 22), a density reported for Shenandoah National Park (Table 23) and the camera area using Bowden's estimator as well (Table 22).

Population estimates using the entire study area proved unreliable due to very low recapture rates between and within summers and the low proportion of marked individuals compared to the whole population (see section above; Bartmann et al. 1987). CABS personnel usually trapped 1 trapline for 2 weeks and then moved on to a new area without returning to the original site for recapture. Population estimates using Chapman's modification of the Lincoln-Petersen estimate therefore had larger confidence intervals than the actual estimate itself and were discarded (Appendix 7).

Open population estimates for the Jolly-Seber (J-S) method could not be rendered at all due to even lower recapture rates. Up to 21% of marked females and 40% of marked males were harvested every year and did not reach the next summer period for re-sampling. In addition, our trapping pattern did not follow the same schedule every year. For example, female 1 might spend June on top of a ridge and move to a valley portion of her habitat in July. One summer she is captured on the ridge in June, but the next year trapping crews do not arrive there until July and miss the opportunity to recapture her. Kasbohm (1994) noted a similar problem with the J-S estimator for population abundance on Shenandoah National Park.

Table 22. Summary of population estimates (black bears > 17 months old) on the northwest study area of the Cooperative Alleghany Bear Study for the summers 1994 – 2000 on the George Washington and Jefferson National Forests, Virginia.

Estimate Type	Population Estimate	Bears / km^2
Lincoln-Petersen (Camera Area [a])	73-76	0.73-0.76
Bowden's Estimate (Camera Area)	63-96	0.63-0.96
Lincoln-Petersen with Harvest-Recaptures (Total Area [b])	582-1,026	0.68-1.19
Lincoln-Petersen (Total Area)	218-519	0.25-0.60

[a] camera-area within total area: $100km^2$; estimates for 1998-2000

[b] total area: $860km^2$; estimates for 1994-1999

Table 23. Black bear densities reported in North America.

Density [a] (bears / km^2)	Area	Source
0.09 – 0.29	Alaska	(Miller et al. 1997)
0.33	Arizona	(LeCount 1982)
0.12 - 0.36	Colorado	(Beck 1991)
0.77	Idaho	(Beecham 1983a)
0.16 – 0.24	Minnesota	(Rogers 1987)
0.2 – 0.5	Montana	(Jonkel and Cowan 1971)
0.21 – 0.35	Tennessee	(McLean and Pelton 1994)
0.70 – 1.09	Western Virginia	This Study
0.67 – 1.04	Central Virginia (Shenandoah National Park)	(Carney 1985)
0.52 – 0.66	Eastern Virginia	(Hellgren and Vaughan 1989a)
0.26	Wisconsin	(Kohn 1982)

[a] reported ranges are year-to-year variations

Population estimate using recovered ear tags during the harvest season

These data, as in most mark-recapture studies, were probably not random in either the marked or the harvested sample. Since most of our trap lines were next to roads, most marked bears either lived next to roads or behaviorally were more likely to be attracted to baits for trapping. Due to hunter access along our trapping routes, harvested bears might therefore have a higher chance of being marked bears. Population estimates derived from a study design where there is a higher probability of capturing (in this case harvesting) a marked bear than an unmarked bear during the recapture period are biased low (Garshelis and Visser 1997). This under-estimation of population size is commonly seen in many mark-recapture studies (Pollock et al. 1990). For this study, we should investigate whether home ranges of radio-collared bears are concentrated around bait sites and roads to determine if we might have underestimated population size by mainly recapturing / harvesting marked bears with overlapping home ranges. Since the methods of marking (summer trapping) and recapture (fall harvest) are different, this bias might be lower than in other black bear studies of mark-recapture.

The harvested (recapture) sample might not be random due to hunter selectivity. Males are predominant in Virginia's black bear harvest (see results; Martin and Steffen 2000) and are actively selected for among Virginia's hound hunters (VBHA member, personal communication; Higgins 1997*b*). A low harvest of females (e.g., of 43 marked females > 17 months old 1 was harvested that fall) by Virginia's hunters might bias this estimation technique. Calculated densities for this estimate of 0.68 – 1.19 bears / km^2 overlap with the estimates for the camera area (0.73 – 0.76 bears / km^2) and from Shenandoah National Park (Tables 22 and 23; Carney 1985).

Population estimate using tetracycline markers

This estimate was used as a control for the harvest data and should have resulted in similar estimates since every hunter is required to submit a bear tooth after a harvest. In contrast to Garshelis and Visser (1997), who found detection rates for tetracycline makers in Minnesota bears of up to 90%, we found considerable variation in detection rate ranging between 35 – 76 % in just 2 years.

Interestingly, bears marked with tetracycline but not detected were mainly older females (> 5years) and younger males (< 4 years). I could not detect a correlation with the amount of tetracycline given since some bears that were not detected had doses twice what is required for them (see General Methods) administered during the summer; bears that were caught more than once received multiple doses. Garshelis and Visser (1997) did notice a decline in detection rate for older bears (e.g., 98% among 1-7 year olds, 74% for 8+ years) and attributed this to thinner depositions of tooth cementum in older individuals. The fact that this trend appeared to be true only for our older females, but not males, might also be related to other factors such as reproduction and nursing, which in turn lowers the thickness of tooth cementum (G. Matson, Matson's Laboratory, personal communication). I am not aware of any published papers on this subject. Further investigation of detection rate, covariates for detection and consistency of detection is needed to make this estimator valid.

Population estimate from camera study

Remote cameras have a long tradition in wildlife research, but have become gradually more prevalent since the development of infrared-triggered systems (Kucera and Barrett 1993). Traditionally, the method has been used for studying feeding ecology, nesting behavior, predation, presence / absence observations, and determining activity patterns (Kucera and Barrett 1993). The use of cameras to estimate population size is becoming increasingly popular (Cutler and Swann 1999). Reasons include a less biased estimate due to differing methods of capture and recapture, and more cost-efficiency in time and money due to decreased trapping and handling efforts. One constraint of this approach is that unmarked animals cannot be marked in resight occasions to increase sample size for future resight occasions; however, the advantage is that resighting is usually cheaper than handling the animal a second time (White 1996). In some species with distinct coat pattern (e.g., tigers) researchers have used this method to estimate population size without ever handling the animal (Karanth 1995).

Within mark-resight analyses, there are 4 commonly used closed population estimation methods including (1) the joint hyper geometric maximum likelihood estimator (JHE) assuming that each animal in the population has the same sighting probability as every other animal during that interval (Bartmann et al. 1987, Neal et al. 1993), (2) the immigration-emigration JHE which allows violation of geographic but, not demographic closure (Neal et al. 1993), (3) the Minta and Mangel estimator, which permits heterogeneity of sighting frequencies by bootstrapping observed frequencies (Minta and Mangel 1989), and (4) Bowden's estimator, which offers an unbiased variance to the Minta and Mangel estimate by basing the variance of the estimate on the variance of resighting frequencies of the marked population (Bowden and Kufeld 1995, White 1996).

I used Bowden's estimate for our analyses because we did not see equal resighting frequencies for our population. Resights varied between 1 and 13 for individuals and were not equal among bears or between sessions. I followed White and Shenk's recommendation to adjust for temporary emigration by adjusting the final estimate by the proportion of observations marked animals spent on the study area (White and Shenk, unpublished manuscript).

This is the population estimate I have the most confidence in because it takes place in a short time frame (i.e., the closure assumption is met), it uses different methods for marking and recapture, reducing the bias that some bears are attracted to bait and others are not, avoiding trap-happy or shyness, and finally it accounts for heterogeneity in resighting probability. Of the 6 estimates we generated during 1998-2000, I am least confident in October 1998 and 1999 estimates because all the resights were based on only 12-14 individuals of 42-45 marked bears (Table 21). The most reliable estimates are probably August 1999 and 2000 due to a higher number of individuals resighted. One reason we might have lower resights of individuals in the October session is that it takes place immediately after the bear dog training season, during which many individuals are displaced from their home ranges temporality (CABS, unpublished data). The August estimates should also meet the closure assumption better since it follows immediately after marking and takes place before the chase season. The August estimates of 0.70 – 1.03 bears / km^2 are similar to previous estimates for Shenandoah National Park, which is 70 km east or our study area (Tables 21 and 23; Carney 1985).

Densities for this 100 km^2 sub-area of the total study area (860 km^2) might be the highest of the total area. My recommendation is to test this camera population estimation in areas where we expect lower densities, such as the southern study area, to evaluate how it performs in lower density areas.

CONCLUSIONS

These analyses suggest that population estimates using mark-recapture data might not be a reliable tool if used on a large area with low recapture rates. During this study, trapping/sampling methods were not specifically designed to generate population estimates. If trapping was designed for population estimates, the validity of estimates over a large area could have been improved. Most reliable population estimates are gained from studies in which > 45% of the total population is marked and during which recapture rates of > 25% are achieved. I believe we achieved this goal for the camera area, in which we trapped very intensively the entire summer and seemed to have marked up to 50% of the population. This is the population estimate I have the most confidence in because it takes place in a short time frame (i.e., the closure assumption is met), it uses different methods for marking and recapture, reducing the bias that some bears are attracted to bait and others are not, avoiding trap-happy or shyness, and finally it accounts for heterogeneity in resighting probability.

Balancing the needs for gaining demographic estimates for an entire area and achieving good estimates of population size is difficult. Priorities have to be set for what we deem important. I believe it was important for CABS to realize we cannot do every thing well at once. If we want valid point estimates to, for example, validate monitoring tools for population change, we need to focus on a smaller area to achieve that goal. However, to observe a trend in Virginia's bear population, the trend would have to be drastic and it would take more than 3 point estimates to detect that change. Population estimation is not exact enough and confidence intervals are too broad to detect a true change unless it is severe. Since we do not have good density estimates from an area with presumed lower population density (southern study area), I believe we should try to obtain that in the last 3 years of the study.

CHAPTER 3. POPULATION MONITORING AND INDICES

Where accurate population data to estimate density are lacking due to time or budget constraints, population monitoring or trend analyses are practical options. Direct counts and accurate population density estimates are difficult to achieve. Both are expensive and time-consuming (Carlock et al. 1983, Caughley 1977). Thus, many states use indices to monitor population changes. These include track counts, scent-station index, harvest trends, damage statistics, vehicle collisions, and others. Indices should be easily applicable and relatively inexpensive (Abler 1988). To ensure the accuracy for predicting population changes by an index, the index has to be tested over an extended period of time and ideally compared to known population sizes (Carlock et al. 1983, Davis and Windstead 1980).

Roseberry and Woolf (1991) suggested a combination of indices, models, and periodical actual assessment of population performance to validate population trends. Garshelis (1990) pointed out that population monitoring for black bears should include a large and varied data set with different monitoring methods. Number of bears harvested is used as a monitoring index in many states, but may not be related to bear population size (Garshelis 1990). A pitfall in many indices for monitoring bear populations is the influence of food availability on the index used, e.g., nuisance activity, bait-station surveys, harvest, and road kill counts (Garshelis 1990). Garshelis (1991) warned that black bear monitoring indices should be evaluated in the context of food availability; food availability indices are conducted by only 13 of 39 states that permit bear hunting.

Our objective for this part of the study was to find 1 or a combination of practical indices that accurately reflect population change and could be used by VDGIF to monitor black bear populations. The indices applied in Virginia at present include a bait station survey, harvest trend data, bow hunter survey, annual vehicle collisions, and nuisance bear activity. To evaluate which indices tracked population trends most accurately, we compared them to population estimates derived from the mark-recapture data in Chapter 2.

METHODS

Relationships among indices were analyzed by correlation analysis (Kleinbaum and Kupper 1978). Each available index was correlated to population estimates (used harvest return estimates since they were available for more than 3 years and were derived from the whole study area; Chapter 2: Table 20) obtained during the same years that indices were recorded. In addition, we evaluated the correlation between mast index and each population monitoring index to determine if the indices were influenced by food availability. If mast index showed a strong negative correlation > $r = -0.60$ (i.e., if mast index availability was low and black bear damage incidence was high) we assumed that food availability could have an influence on this index in relation to population size.

Bait station survey

VDGIF and CABS personnel conducted a bait station survey during 1995-1999 that followed the guidelines of the Tri-State Bear Study (Carlock et al. 1983). Every August, the same 25 transect lines of 10-20 bait stations (total stations 246-261) were placed across the northern study area. A bait station consisted of 3 sardine cans tied on a string and suspended from a tree limb 3.3 m high and 1.3 m away from the tree trunk. After 5 days, we checked each station and recorded whether sardine cans were taken by a bear, non-target animal, or not visited at all. Assumptions of this index are that observers can identify bear visits and that visitation rates are not influenced by natural food availability and only fluctuate with population size.

Nuisance bear activity

This index consisted of the number of bear damage complaints registered with VDGIF every year. This was a state-wide index because data for individual counties were not available to the author. An assumption was that with increasing population size more nuisance activity exists with bears in search of food. This index can be confounded by a poor mast year that forces bears to search for food in agricultural areas or by inconsistent reporting rates.

Black bear harvest

Harvest data, provided by VDGIF, were broken down into bow harvest, general rifle season (no hounds used), and hound-season. VDGIF requires that bears are checked at specific check stations.

Vehicle collision statistics

VDGIF game wardens, County Sheriffs, and Virginia State Police provided VDGIF biologists with incidental observations of bears killed on roads and highways by vehicle collision. Many bears that are killed on highways are probably not found because they are able to walk away from the road into near vegetation and die or are taken by people before they can be collected by official personnel. I personally observed such an incident on the northern study area and was lucky to record the ear tag number before the bear disappeared. However, if the reporting rate is consistently low it might still be a valid index. Possible confounding factors are fluctuations in the number of vehicles on a given road causing more or fewer bear-car accidents, that bears encounter more roads by roaming larger areas in search of food in a poor mast year, or that road density increases in bear habitat over time.

Bow hunter survey

VDGIF conducts a bow hunter survey of deer hunters to determine how many bears are observed during the bow season. The assumption is that with higher bear numbers, bow hunters will sight more bears. Possible causes for inaccuracy of this index could be food availability and weather.

RESULTS

Bait station survey

In 2000, 59 of 264 (22.3%) baits were taken and bears visited 7 additional sites. Visitation rates for previous years were 11.5% in 1995, 12.5% in 1996, 22.0% in 1997, 13.8% in 1998, and 29.5% in 1999. The distribution of hits for the bait station survey is noteworthy; there appeared to be a north to south distribution of hits within the northern study area. Transects that received the most hits by bears were all northern transects ($\bar{x}$ = 5.7 hits / transect; Sand Springs Trail is cut-off between north-south). Southern transects had fewer or no bear hits ($\bar{x}$ = 1.5 hits / transect). Visitation rate of bait stations and population estimates (Chapter2: Table 20) were highly correlated ($r = 0.97$, $n = 5$, $P = 0.007$; Table 24, Fig. 8).

Nuisance bear activity

Damage complaints registered with VDGIF ranged from 62 in 1996 to 127 in 1997 (Martin and Steffen 2000). Correlation with population estimates was $r = 0.58$ ($N = 5$, $P = 0.303$; Table 24).

Black bear harvest

Virginia's black bear harvest has continually increased since 1994 (Chapter 1) and is only weakly correlated with population estimates ($r = 0.49$, $n = 6$, $P = 0.328$). However, when total harvest was divided into archery, non-dog, and dog harvest, there was a strong correlation between the archery harvest and population estimates ($r = 0.95$, $n = 6$, $P = 0.002$; Table 24). Correlation between archery harvest and mast index was $r = -0.65$ ($n = 6$, $P = 0.160$).

Vehicle collision statistics

In 1997, 31 bears were recorded killed by automobiles on Virginia's highways, whereas in 1996, only 22 were recorded (Martin and Steffen 2000). Correlation between population size and vehicle incidents was moderate ($r = 0.76$, $n = 5$, $P = 0.140$; Table 24).

Table 24. Pearson's correlation coefficients between population estimates (Chapter 2: Table 20) and Virginia's mast index with population monitoring indices collected in Virginia between 1994 and 1999. Raw data see Appendix 8.

Index	Population estimate	*P*	Mast index	*P*
% Baits taken by bear	0.97	0.007	-0.45	0.448
Vehicle collisions	0.76	0.140	-0.33	0.590
Mast index	-0.55	0.263	1.00	--
Archery harvest	0.95	0.002	-0.65	0.160
Non-dog harvest	0.20	0.709	-0.44	0.388
Dog harvest	-0.06	0.905	0.16	0.763
Total harvest	0.49	0.328	-0.39	0.448
Damage complaints	0.58	0.303	-0.57	0.314

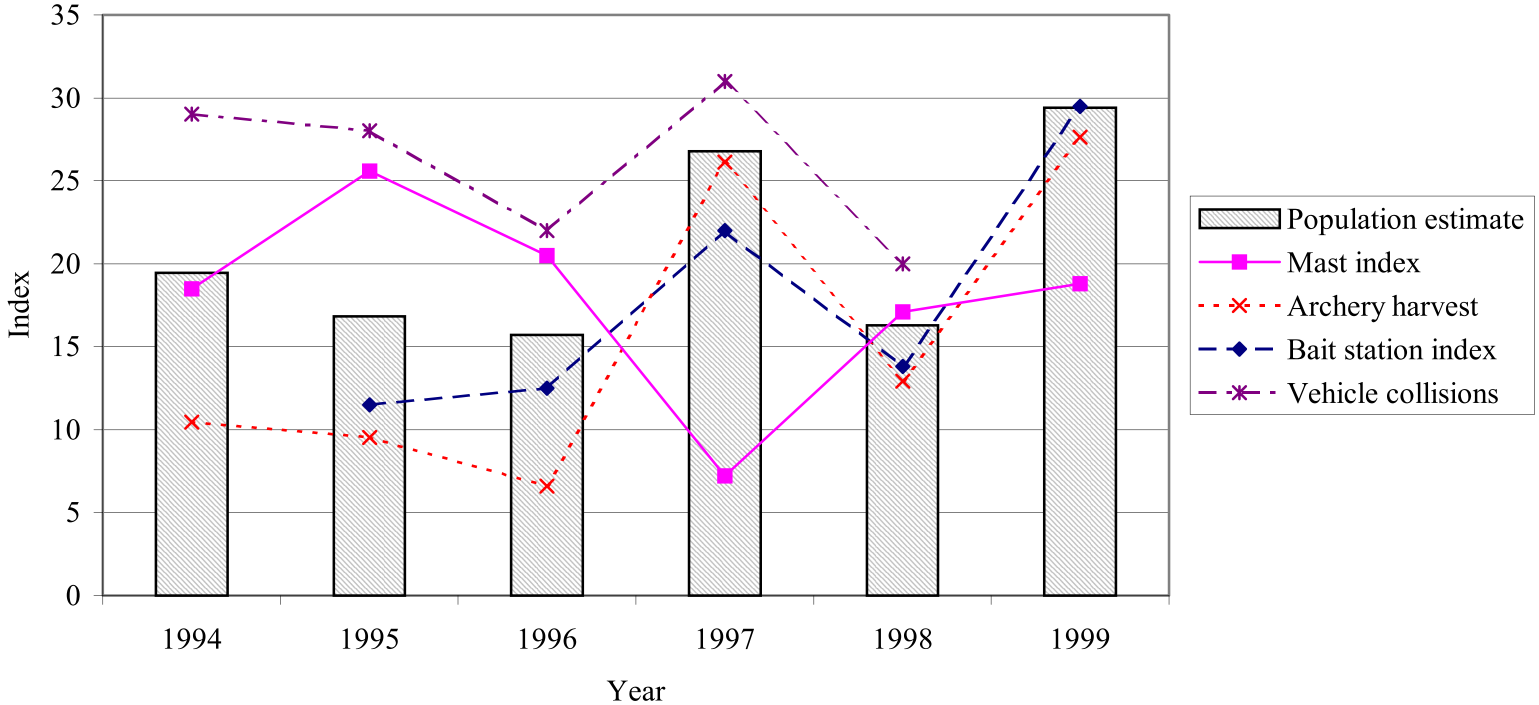

Figure 8. Population monitoring indices, 1995-2000, and population estimates (scaled to fit chart: raw data Appendix 8; dead return population estimates from Chapter 2) for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

DISCUSSION

Population estimates and trends are important data managers use for population management. Much research has been focused on development of effective population monitoring tools (Gibbs 2000). Few studies have validated relationships between commonly used indices, such as bait station index, or harvest numbers, and population size estimates for bears, probably due to the lack of long-term intensive trapping studies (Garshelis 1993). In Virginia, we were fortunate to have population estimates overlapping with monitoring indices to evaluate their relationships.

Bait station survey

Johnson (1992) reported that bait station indices correlated well with the Jolly-Seber population estimates from Great Smoky Mountains National Park (GSMNP). Bait stations are used in several southern states and have proven to be an economical and reliable index of relative black bear numbers (Johnson 1992, Kohn 1982). Pre-bait visitation rate in areas with regular and extensive trapping was also a reliable monitoring method in Arkansas, but expensive and labor intensive (Smith 1985). However, Miller (1993) reported that bait station surveys in southern Mississippi, an area with low bear densities, were not successful due to low visitation rates.

For our study, the bait station index seemed to correlate well ($r = 0.97$, $n = 5$, $P = 0.007$) with mark-recapture population estimates from the same area. Garshelis (1990) cautioned that visitation rates of bears to bait sites can be biased if bait sites are not independent from each other. We located bait sites 0.5 miles from each other on alternating sides of transect lines (often ridges) to avoid that bears can smell baits between bait sites. In addition, van Manen et al. (unpublished manuscript) also pointed out that if population densities are high and visitation rate is >25%, chances are high that a bear will encounter a bait station that has already been visited by another bear. This was not observed in our study with visitation rates staying below 25% except in 1999.

Van Manen et al. (unpublished manuscript) did not find a good correlation between bait station index and population estimates, but they pointed out that both their estimates and indices were derived from trap lines on mountain ridges in Great Smoky

Mountains National Park (hiking / access trails are located mostly on ridges within the park). They conceded that in bad mast years bears might not visit ridge tops, but will be located remain in the valleys where they did not trap. In our case, trap and bait station lines were interspersed in all terrain and habitat types within the study area, which might offset any distribution changes (e.g., only in valleys) due to lack of food in certain parts of the study area. Another indication that oak mast does not influence the bait station index is the weak correlation between them ($r = -0.45$, $n = 5$, $P = 0.448$). In 1997, mast index was recorded at a poor or failing level and visitation of bait stations was high (22%). However, mast production was high in 1999, yet visitation rate of bait stations was at an all time high of 29%. It will be important to continue bait station surveys to see if these relationships hold true beyond 5 years.

Nuisance bear activity

Conflicts between humans and black bears are common throughout the bears' range. Bear-human interactions include damage to property (bird feeders, trash cans, houses, vehicles), agricultural crops (corn, apiaries or orchards), livestock depredation (mainly sheep), and aggressive encounters in recreation sites such as National Parks (Kasbohm 1994, Martin and Steffen 2000, Vaughan et al. 1990). In Virginia, counties around Shenandoah National Park are mainly affected by orchard and corn damage, whereas other kinds of damage are dispersed around the state (Martin and Steffen 2000). The level of nuisance activity can be influenced by natural food abundance (Beeman and Pelton 1980, Garshelis 1989, Rogers 1976b). Damage complaints in Virginia were only weakly correlated with population estimates ($r = 0.58$, $n = 5$, $P = 0.303$) and mast index ($r = -0.57$, $n = 5$, $P = 0.314$).

We expected that with increasing population size prime habitat would become limited and bears would be more likely to seek food closer to humans. In addition, we expected that when natural food (e.g., mast) was in low abundance, bears would find alternative food sources such as corn or fruits in orchards.

Several factors may explain the low correlation between damage complaints, population size and mast index. First, damage complaints are mainly registered in counties outside the study area. Most damage occurs around Shenandoah National Park.

Our study area is located almost exclusively on National Forest land with little opportunity for human-interaction. Second, Shenandoah Park is a narrow park with some areas only 4-6 miles wide. Home ranges of bears (especially males) are larger than the width of the park and naturally include agricultural landscapes (Garner 1986). Bear populations in the park might not have to have high densities for bears to leave the park. Third, bears can become habituated to humans and their food sources (Herrero 1985). Finding food in orchards and cornfields at peak harvest times is probably easier than finding spotty food patches in the forest. When bears become accustomed to this food source they might prefer it over natural foods, regardless of population size. No such food preferences have been tested, but seem obvious. Therefore, damage complaints might not be related to natural food availability, but food preferences of certain individual bears. Nuisance bear activity might therefore not be a good index for population levels, except when populations grow close to carrying capacity of the natural habitats and bears have to disperse into marginal habitats from other areas (density – dependent processes).

Black bear harvest

Harvest levels have been used as an index to population size for many years and by many agencies (Garshelis 1990). The index assumes that harvest increases with population size. In Virginia, we found only a weak correlation between the total black bear harvest and population size ($r = 0.49$, $n = 6$, $P = 0.328$). Several factors such as weather, hunter participation and hunter success can influence harvest. The late hunting season is especially susceptible to cold, snowy weather, and might cause bears to den earlier and making them unavailable for harvest. In addition, harvest numbers were totals for the state of Virginia and not specific to the 2 counties the population estimates were derived from. County specific data was not available from VDGIF at the time of these analyses but should be used in future evaluation of these indices.

When the harvest was divided into individual seasons, there was a strong correlation between archery harvest and population size ($r = 0.95$, $n = 6$, $P = 0.002$). Data were not available on hunter effort for archery hunters, but might be worth investigating. If archery hunter effort has been constant and harvest is correlated to population size, we should expect an increasing archery harvest with increasing population size. The archery harvest in Virginia has steadily increased over the last 6 years from 89 bears taken in 1994 to 235 in 1999. In years of poor mast, archery harvest increased (1997) yet in 1999, a good mast year, archery harvest was still high. The weak correlation between the mast index and archery harvest ($r = -0.65$, $n = 6$, $P = 0.0.160$) indicates that mast failure might influence archery harvest, but is not the sole determinant. Again, factors such as weather (rain fall, snow) might clarify this relationship.

Harvest sex ratios are a primary monitoring tool for black bear populations in the west (Garshelis 1993). Many states have guidelines suggesting that female black bears should constitute no more than 40% of the harvest to maintain a stable or increasing population. To lower the number of females in the harvest, many states avoid early fall hunts when females are not denned or the use of early spring hunts when females have not emerged (Garshelis 1993). An increasing percent of females in the harvest is generally considered (and often wrongly) a sign of over-harvest and a decreasing population trend (Garshelis 1993). Garshelis (1993) pointed out that states with large, healthy bear populations, such as Maine, Minnesota, and Pennsylvania, regularly report harvests with more than 40% females. To achieve a continually male-biased harvest, a state would have to experience a male-biased recruitment. If a 1:1 sex ratio is assumed and if male bears do not reach older age classes because they were harvested early in life, it follows that females will become more prevalent in older age classes. If females are continuously less represented in the harvest, yet a hunter preference is male-biased (which should result in an increased proportion of females in the older age classes of the harvest), the skewed sex ratio can be an indication of an increasing population (Garshelis 1993). Sex ratio changes in the harvest that have not been caused by hunting regulation changes can generally be considered a change in population status. However, researchers should always be aware that temporary changes in harvest sex ratio can be influenced by weather, hunting participation, food supply and should be considered carefully (Garshelis 1993).

In Virginia, the percent females in the harvest decreased from an average of 46.4% during 1962 - 1973 to 38.6% during 1974 - 1999. This change, however, was attributed to a change in the hunting regulations in 1974, which shortened and delayed the bear hunting season by 2 weeks in the fall, giving females a better chance to den by the time hunting season started (D. Steffen and D. Martin, VDGIF, personal communication). Percent females taken between 1974 and 1999 ranged from 29.4% in 1979 to 49.5% in 1974. There seems to be no clear pattern to explain the proportion of females taken. As noted above, these changes will be very difficult to interpret unless a drastic change persists over several years. I did not include this index into my analyses because no clear trend was evident in Virginia's harvest data.

Harvest age structure is another index commonly used to monitor exploited populations. Generally, an increasingly younger population is considered overexploited. However, Garshelis (1993) showed several cases where this is not so. For example, in populations where females with cubs are protected, pre-reproductive females are harvested more often, do not reach the older age classes and make the female population increasingly older. Garshelis (1993) recommended interpreting age data very cautiously in connection with other population trend data and in general believed that age structure is too unpredictable to be used as a reliable index. I did not include these data because age-specific harvest data were not available from VDGIF in time for these analyses.

Vehicle collision statistics

Human injury by deer-vehicle collisions is a common and costly problem. Economic losses can be substantial in addition to loss of life (Romin and Bissonette 1996). Compared to an average of 3,427 deer killed on Virginia's highways annually (Romin and Bissonette 1996), bear-vehicle collisions are very rare. Martin and Steffen (2000) reported vehicle collisions during 1980 – 1999 ranging from 20 in 1998 to 31 in 1999. These numbers are probably minimum estimates since there is no standardized reporting protocol between VDGIF biologists and game wardens, state and local police, and Virginia Department of Transportation (VDOT). We recorded 3 road killed bears within our study area that were not reported by any of the above. One problem probably is that road killed bears are picked up frequently by private citizens for parts (e.g., skull and claws) before they are reported by state officials. Police reports of wildlife - vehicle accidents do not document the specific species (e.g., bear, deer). Insurance claims for bear damage to vehicles would be another way to receive a more complete estimate of bear-vehicle collisions, but might be under customer confidentiality and not available. In addition, bears might damage a vehicle, but not die from the impact. CABS handled an adult female in 1999 that showed healing of a compound fracture in her right hind leg that could have stemmed from a vehicle collision. Correlation between vehicle collisions and population size was moderate ($r = 0.76$, $n = 5$, $P = 0.140$) and could be confounded by dispersal of subadults. Adult bears that have established home ranges in areas without major roads may be less likely to be killed by a car accident than dispersing subadults in search of a new home range. Comly and Vaughan (1997) found that vehicle collision was the major mortality source for translocated bears in Virginia, which could be similar to dispersing subadults.

CONCLUSIONS

Monitoring population trends in an important aspect of population management. Good monitoring indices should be easy to apply, inexpensive and reliable to portray change in population trend. Many scientists caution against using just one index alone as a monitoring tool (Garshelis 1993). Indices on their own are inherent to confounding factors that might bias them. For example, during years of low food availability, bait sites might be visited more frequently by bears due to larger distances traveled in search for food rather than an index of larger population size.

Population indices that could aid in monitoring Virginia's black bear populations seem to be the bait station index, archery harvest, damage complaints and vehicle collisions. Bow hunter surveys are conducted, but were not available from VDGIF at the time of the analyses and should be considered in the future. In our study, all of these indices pointed in the same direction of a population increase (Fig. 8). However, Anderson et al. (2001) pointed out that a risk in data analysis exists when sample size (n) is small relative to the number of parameters being estimated. To construct a directly proportional regression function (rather than keeping it a correlation analysis) for population size increase is a dangerous proposition and should not be attempted with only 5-6 years of data. However, population management should not rely on indices alone in the long term. Periodic population estimates are an invaluable calibration tool for the trend estimates of the indices. I recommend periodic estimates such as an intensive trapping effort every 5 years and using harvest returns as recaptures for mark-recapture analysis. The trapping effort would have to be conducted in the same area every time, however, to make it a valuable estimate for comparison. The indices here were correlated to estimates from the camera area within the northern study area, which could be the future monitoring area for Virginia's black bear population.

CHAPTER 4. DEN-TYPE USE AND FIDELITY OF AMERICAN BACK BEARS IN WESTERN VIRGINIA

Studies of the denning ecology of American black bears traditionally have focused on den type (e.g., trees, ground dens, excavations, rock cavities), den site and habitat characteristics, and denning chronology. Studies investigating reuse of individual dens have found it to be low: 4.8% in Pennsylvania (Alt 1984*a*), < 1% in Alberta (Tietje and Ruff 1980), and no reuse in Ontario (Kolenosky and Strathearn 1987). Several studies have reported a high rate of den reuse, which authors attributed to low den availability (Schwartz et al. 1987, Lindzey and Meslow 1976). Fidelity to one specific den type has been reported for polar bears (Amstrup and Gardner 1994), but has not been investigated for black bears and their offspring. We suspect the paucity of studies reflects the requirement of a long-term study that follows individuals over several years, and the difficulty in marking and following their offspring. In Virginia, black bears den in hollow tree cavities, tree stumps, rock cavities, in excavations under root systems, under log and brush piles, in intricately constructed nests, and in simple day beds. The denning period typically occurs between the middle of November and early April (Godfrey 1996, Ryan 1997). Godfrey et al. (2000) reported that 72.2% of bears monitored in Virginia between the winters 1995–1997 used tree dens, although rock cavities were readily available for denning.

Our objectives were to determine (1) den-type use of adult bears, (2) if adult bears were faithful to den type, (3) if offspring used the same den type as their mothers, and (4) if den type choice was influence by sex, age, size, study area, mast crop, and/or reproductive status. Our predictions were that larger, older bears would den in trees less often than smaller, younger bears. We predicted that in years of good mast crop bears would den in rock cavities and on the ground due to more weight gain and limitations imposed by tree cavity size. We also hypothesized that females with yearlings would be more likely to den on the ground than in trees due to the same cavity size restrictions. We suspected that habitat differences (stand age) and land ownership (public vs. private) on the 2 study areas would influence den choice. Bears are hunted with hounds in Virginia during December and January; we hypothesized that they might use trees to reduce detection during the hunting season. Understanding the importance of tree dens can aid in the management and conservation of Virginia's bear population.

METHODS

Capture, Handling, and Radio Telemetry

We captured bears with Aldrich foot snares and culvert traps from May 1994 to August 2000. Each bear received plastic ear tags and a lip tattoo. We recorded weight , sex, and reproductive status, extracted the first premolar to determine age by cementum annuli analysis (Willey 1974), and examined females for lactation or signs of estrus (e.g., swollen vulva, discharge). We injected bears with a tetracycline antibiotic (200 mg/mL) at 4 mL per 44 kg to prevent post-capture infections.

Bears were equipped with motion-sensitive radio-transmitters (ATS, Isanti, MN; Lotek, Quebec, Canada; Telonics, Mesa, AZ; Wildlife Materials, Carbondale, IL) that included a cotton breakaway device (Hellgren et al. 1988). Starting in 1999, yearlings and large males received ear tag transmitters (ATS, Isant, MN) to avoid ingrown collars in fast-growing individuals. We marked 305 cubs with lip tattoos and fitted 118 (those with weight > 1.7 kg) of them with expandable radio collars designed by CABS personnel (unpublished data). We located dens using ground and aerial telemetry.

Den Work

From November to January each year we determined the type of den (i.e., tree, rock cavity, excavation, slash-pile, open ground nest) radio-collared bears were using. Reproductive status was estimated from trapping data during the previous summer or from past reproductive history. Dens of adult males and females with yearlings were not located beforehand because they often denned in open ground nest and were difficult to approach. Once a bear has been disturbed in its den it is very difficult to successfully handle in succeeding attempts. We handled males, females with yearlings, lone yearlings, and barren females during January–February, and pregnant females during March–early April. We entered tree dens by cutting a window into the tree if we could not reach the bear from the entrance hole (Godfrey et al. 2000). The logistics of handling bears in tree dens did not allow us to randomly sample weights.

Mast Crop Evaluation

The Virginia Department of Game and Inland Fisheries has conducted quantitative mast crop surveys in Virginia since 1971 (Coggin and Peery 1971). The sampling protocol calls for 4 plots per county with plot 1 at the foot of a typical ridge in the area, plot 2 about half-way up the side of the mountain, plot 3 on top of the ridge and plot 4 on the other side of the ridge at the same elevation as plot 2. Mast crop was evaluated by counting acorns on the last 53 cm of 10 branches chosen at random on 10 white oak and 10 red oak trees per study plot during the last week of August. Trees had to have full crowns in direct sunlight and have a DBH larger then 18 cm.

Mast crop was reported as an average number of acorns per limb from the 20 trees per plot and averaged across plots for one cumulative score per county. Individual values for white and red oak mast were available, but were ignored for this analysis.

Data Analysis

We used χ^2 tests of independence to evaluate if denning in trees (vs. other) was independent of sex and of study area, and to test if den-type selection differed among age classes (Sokal and Rolf 1995). A Mann-Whitney U test was used to test for a difference in age of bears captured on the 2 study areas. We report actual significance levels from statistical tests except where $P < 0.001$.

We used a proportional odds model (POM), a class of ordinal response models, to test if den choice was related to sex, age, study area, mast crop, and reproductive status (pregnant, with yearlings, lone). An ordinal response is a categorical variable that is multinomial (i.e. in our case several den types) and not independent. The POM is similar to a logistic regression analysis except that the response values (ordinal values) are related to each other in a specified order. The POM can test interactions between variables similar to a regular regression model analysis (Schabenberger and Pierce 2002). The order of responses that is necessary for an ordinal response model in our case was related to den type. We ordered den types in what we assumed to be decreasing order of 'security against disturbance' as follows: trees (most secure; ordinal value = A), rock/excavation cavities (moderately secure; ordinal value = B), and open dens (least secure; ordinal value = C). A POM was fit by PROC GENMOD (SAS Institute® 2000) using a multinomial distribution. The significance of a variable (sex, age, study area, mast crop, and reproductive status) in den choice was given by a likelihood ratio test (χ^2 values).

RESULTS

Den type use

CABS handled 83 individual adult black bears and 237 cubs in 142 dens in the northern study area and 36 individuals with 85 cubs in 56 dens in the southern study area throughout the winters of 1995 to 2001. Sixty percent of handled bears denned in tree cavities (68% of located dens; Table 25). In the northern study area, the proportion of females using tree dens (65%, n = 127) was larger than the proportion of males using trees (33%, n = 15; χ^2 = 10.69, df = 1, P < 0.001; Table 25). However, when we pooled both study areas, the proportion of bears using trees as dens did not differ between sexes (χ^2 = 1.55, df = 1, P = 0.214). The proportion of bears using tree dens did not differ between study areas (n = 203, χ^2 = 1.63, df = 1, P = 0.202). Ground dens included nests in laurel thickets, excavations, brush piles, and rock cavities.

Sex and age, but not study area or mast crop were important factors in determining the type of den a bear selected (Table 26). The reproductive status of females was not significant in den choice (POM: n = 133, χ^2 = 0.0818, P = 0.853). We

Table 25. Den-type selection by sex and area for black bears of the Cooperative Alleghany Bear Study, George Washington and Jefferson National Forests, Virginia, during 1995–2001.

Sex	*n*	% Tree	% Rock cavity	% Open
Female				
Northern	127	65.4	18.9	15.7
Southern	54	51.9	42.6	5.6
Total Female	181	61.3	26.0	12.7
Male				
Northern	15	33.3	40.0	26.7
Southern	8	75.0	25.0	0.0
Total Male	23	47.8	34.8	17.4
Total	204	59.8	27.0	13.2

Table 26. Ordinal response regression for den-type selection of black bears (n = 188) within the Cooperative Alleghany Bear Study, George Washington and Jefferson National Forests, Virginia, during 1995–2001.

Parameter	DF	χ^2	P
Area	1	1.07	0.302
Year	1	0.36	0.548
Sex	1	3.76	0.053
Age	1	22.40	< 0.001

tested for interactions between age and sex, age and reproductive status, age and area, and area and sex in den type selection (POM analysis), but all were insignificant and therefore dropped from the analyses to increase degrees of freedom for the analysis and power of the test (Schabenberger, personal communication). The average age of bears handled in the northern area ($\bar{x}$ = 7.8 yr) was older than in the southern area ($\bar{x}$ = 6.0 yr; T = 4347.0, P = 0.001). Den-type selection differed among age classes (Table 27; χ^2 = 19.86, df = 4, P < 0.001); bears < 6 years old denned in rock cavities less then expected (expected value = 16, observed value = 7), whereas bears >10 years old denned in rock cavities more than expected (expected value = 13, observed value = 22).

Den type fidelity by individual bears

From 1995 to 2001, 53 bears in the north and 13 in the south were handled for 2–6 consecutive years. Twenty-six (39%) bears consistently used tree dens, 8 (12%) bears were faithful to rock cavities, and only 4 (6%) bears continuously used ground dens. Twenty-eight bears (42%) switched den types over the 6–year period, primarily from tree dens to rock cavities (18%) or to open nests (18%). Twenty-five of 26 bears consistently using trees were female, 25 of 26 weighed < 82 kg, and 24 of 26 were < 10 years old. Only 3 males stayed faithful to den type, 1 for each den type. Switching den types did not seem to be correlated with reproductive status. We observed 2 females that had produced cubs in rock cavities denning in trees with yearlings. Two females denned in trees when producing cubs but constructed day-bed nests when with yearlings.

We followed 5 bears marked as cubs in their dens to adulthood. All 5 showed the same den type preferences as their mothers. One male denned in an open nest and was born under a rock outcropping, 2 females chose trees like their mothers, and one female denned in a rock cavity similar to her birthplace.

We recorded 9 incidences of den-reuse by radio-collared bears; 3 females reused their previous den trees (one female for 3 consecutive years), 1 female returned to a rock cavity during a cub-bearing year (she denned in a tree with yearlings between cub-bearing years), and 1 male used the same rock cavity as the previous year. The other 4 incidences involved different bears (3 study animals and 1 previously not captured bear) using tree dens that had been previously occupied by study animals. None of the reuse

Table 27. Den-type selection by age class for black bears of the Cooperative Alleghany Bear Study, George Washington and Jefferson National Forests, Virginia, during 1995–2001[a].

Age class	*n*	% Tree	% Rock cavity	% Open
< 6	58	74.1	12.1	13.8
6 – 10	73	60.3	28.8	11.0
> 10	48	35.4	45.8	18.8
Total	179	57.5	27.9	14.0

[a] discrepancy in total number of bears to Table 25 because not all ages could be determined.

trees had a window cut to handle the bears in preceding years.

DISCUSSION

This study revealed several patterns in den type use and fidelity of black bears in Virginia that can aid management. Although other variables such as weight and habitat availability should have been included in the analysis, circumstances prevented their inclusion.

Den type use

Black bears den in trees primarily in the southeastern United States (Wathen et al. 1986), but also use tree cavities in Pennsylvania (Alt 1984*a*), Arkansas (Oli et al. 1997), Michigan (Switzenberg 1955), and Washington (Lindzey and Meslow 1976). In the Appalachian region, up to 71% of black bears den in tree cavities above ground (Godfrey et al. 2000, Kasbohm et al. 1996, Wathen et al. 1986). Our data show a slightly lower use of 60% of handled bears denning in trees.

Female black bears were more likely to use tree dens than males in our northern study area, but no difference was observed when both study areas were pooled. We hypothesize that we did not find a difference between males and females using tree dens because of the lack of large males (> 160 kg summer weight) in our sample. We recommend an increased sample of large males in future studies of den selection.

Sex and age were significant factors in determining the type of den selected. Bears > 10 years old denned in rock cavities more often than expected. Godfrey (1996) reported an average diameter of 52.7 ± S.E. 2.7 cm for tree cavities compared to an average ground nest diameter of 80.7 ± S.E. 5.5 cm used by black bears on the GW&JNF during 1995─96. We speculate that older, larger bears cannot find tree cavities large enough for denning and are forced to use ground dens instead. The significance of age in our POM analyses might be related to increased weight with age. We could not quantify this relationship between age and weight due to above-mentioned sampling bias of lighter bears in dens, but a relationship of a size threshold for denning in a tree cavity seems reasonable. If larger trees limited, the older segment of our bear population might use more tree cavities for denning if they were available.

Study area was not a significant factor in den tree selection of black bears. However, a larger proportion of female bears than male bears denned in trees on the northern study area. The northern study area has a larger portion of contiguous wilderness, roadless areas, and National Forest with more mature timber that is more difficult to extract than on private lands of the southern study area, and therefore might have older, larger trees. Conversely, the southern study area is highly fragmented with several tracts of timber company land. Ryan (1997) reported that 43% of radio-collared bears on the southern area denned on private land, which composed about 50% of the total study area. We recognize the need to assess den tree availability to verify this relationship.

Earlier investigations suggested that black bears can increase their productivity by choosing tree dens that provide energetic savings from thermal insulation (Johnson et al. 1978) and a reduced chance of cub mortality due to cavity flooding (Alt 1984*b*). Others, however, did not find a difference in litter size among bears in different den types (Hellgren and Vaughan 1989, Rogers 1987). Bears in the northern hemisphere give birth during the winter, leaving them vulnerable to disturbances, which would increase energetic expenditure (Linnell et al. 2000, Ramsay and Dunbrack 1986). Human disturbance by approaching dens during hunting or radio-tracking may cause bears to abandon their dens and cubs (Poelker and Hartwell 1973, Reynolds et al. 1976). Weight loss of up to 25% for reproductive females during hibernation limits the amount of energy that can be allocated to disturbance-induced activities such as den relocation (Tietje and Ruff 1980, Erickson and Youatt 1961, Hock 1960). Because bears are hunted with hounds in Virginia during December and January, denning in trees might reduce the chance of disturbance by humans (Alt 1980). The effect of disruption to bears in ground dens by hound hunters is difficult to estimate.

Den type fidelity

Five of 9 instances of den-reuse were by the same individual. Alt (1984*a*) reported 41% of all reuse cases in Pennsylvania were by the same bear, and 11% by a relative of the previous bear. In the remaining 4 instances, the relationship between occupants was unknown. However, because all offspring used the same type of den as their maternal site, we believe it likely that offspring could occupy their maternal den in the future. We point out that although we disturbed these bears by handling them in the dens, they returned to the same denning location within 1-2 years of handling. However, none of the trees that were reused had been cut by chainsaws to access the den.

MANAGEMENT IMPLICATIONS

Our findings emphasize the importance of den trees for Virginia's bear population. Rock cavities appear to be readily available, yet 60% of handled bears used trees. Hunters have reported that dogs can find denned bears on the ground, but do not detect them in trees (Virginia Bear Hunters' Association member, personal communication). The fact that older, larger bears switch from tree to ground dens might indicate a lack of large enough den trees. The protection provided by large den trees may be an important factor in the dynamics of Virginia's hunted black bear population. In addition, an evaluation of the effects of research activities (e.g., cutting a window in a den tree, handling a bear, radio-tracking) on den sites might be appropriate if den trees are not reused after handling for a longer period of time than den trees that were not accessed for research activities.

CHAPTER 5. MODELING POPULATION GROWTH CHANGES FOR VIRGINIA'S HUNTED BLACK BEAR POPULATION

Models are an abstract representation of a natural system or process that can help us understand data of a complex system, test our understanding of that system, and make predictions for the future (Starfield and Bleloch 1986). Some researchers rely on modeling of animal population dynamics as an essential management tool (Gross 1972, Pojar 1981). Roseberry and Woolf (1991) argue, however, that managers should verify and validate models with independent assessments of population status before applying them to management. Models can vary in detail depending on the understanding we have of the problems we are trying to solve and the quality and quantity of available data when building a model (Holling 1978). Most non-physical sciences tend to have problems when the understanding of a problem / system is incomplete, and the available data are sparse or biased (Starfield and Bleloch 1996).

Only a few population models specific to bears currently exist (McLaughlin 1998). Knight and Eberhardt (1984) and Shaffer (1983) built models to project grizzly bear (*Ursus arctos*) population size. Harris et al. (1986) developed a generic stochastic population model and used it to simulate grizzly bear population dynamics. Taylor et al. (1987) designed a model (ANURSUS) to estimate population parameters for North

American bear species, based on age-specific observations of litter size. McLaughlin (1998) developed a stochastic population model simulating the effects of food and harvest on female black bears in Maine. The latest projection model, developed by ESSA Technologies Ltd. (2001), is based on life-table data for black and polar bears. It can incorporate Monte Carlo estimates of the uncertainty of similar results, plus it allows for density-dependent effects on specified parameters.

Population viability in general relies on the recruitment of reproducing females into older age classes. Black bears have been known to reproduce continually for up to 25 years in the wild (McLaughlin 1998). Reducing the breeding population can lead to rapid population decline and slow recovery due to late sexual maturity and low reproductive rate in bears (Miller 1990). Management agencies therefore use conservative approaches to harvesting bears because biological and social consequences of over-harvest and declining populations can be detrimental (Miller 1990). Understanding the dynamics of the female population is consequently very important for effective management.

The overall goal of the modeling exercise presented was to help us understand population dynamics of Virginia's hunted black bear population, and to aid VDGIF in achieving population goals specified in Virginia's black bear management plan. These include the stabilization of population growth in Rockingham and Augusta counties where the north study area of CABS is located (Virginia Black Bear Management Plan 2001-2010, 2001). The first objective for this study was to evaluate the influence of demographic parameters (reproduction and survival) on the growth of Virginia's hunted black bear population. Secondly, we wanted to investigate how changes in harvest rate (controlled or uncontrolled) with current estimates of survival and reproduction (Chapter 1) can affect population growth. The third objective was to project the population size of Virginia's hunted black bears into the future with simulated changes in survival below current estimates that could result from to changes in factors such as mast production, hunter effort, or hunting season.

METHODS

Model Parameters

I used female survival and reproductive estimates from Chapter 1 (Table 28) and assumed mean litter size of 2.35 cubs / litter for adults, 1.1 cubs / litter for 3-year-old bears, and a cub sex ratio of 1M:1F. An annual adult female reproduction is therefore:

$\left(\frac{2.35 cubs}{litter}\right)/4 = \frac{0.575\, femalecubs}{year}$ (assuming bears reproduce every other year).

Low annual survival rates (Table 28) were the lower 95% confidence interval bounds from the mean estimates and were used to simulate an impact of change in mean annual survival rate that could be due to factors such as change in hunting regulations, lower mast production or lower hunter effort.

Objective 1. Sensitivity analysis of live-history parameters for female black bears in Virginia's hunted black bear population.

I used a life–stage based Leslie Matrix (also called Leftkovich / Usher Matrix) consisting of 5 age classes, including cubs (0-1 year), yearlings (1-2 years), 2-year-olds, 3-year-olds, and adults (> 3 years; Fig. 9; Caswell 1989, Manly 1990, Usher 1972). I kept separate age class categories for 2 and 3-year old female bears (rather than combining them as 'subadult bears' because we did not observe reproduction in 2-year-old bears). This model is based only on females with the assumption that male bears are not limiting the reproduction of females (i.e., there are always enough males to fertilize all receptive females; Caswell 1989). Population growth rate (λ) was calculated by the dominant Eigenvalue of the Leslie matrix (Gotelli 1998).

To determine how changes in reproduction and survival of female black bears influenced population growth of Virginia's hunted black bear population, I changed one parameter (sex– and age–specific survival and reproduction, Fig. 9) at a time at set increments (reproduction: 0.01; survival: 0.10), while keeping all other parameters constant.

Table 28. Input parameters for Leslie Matrix population model (based on females only) of Virginia's hunted black bear populations as estimated between 1994-1999. Reproduction only includes female cubs born / year. High and low values are upper and lower 95% C.I. bounds from estimates in Chapter 1 (Tables 6 and 14).

Age Class	Average Reproduction / Year	Low Reproduction / Year	High Reproduction / Year	Average Annual Survival	Low Annual Survival	High Annual Survival
Cub	0.00	0.00	0.00	0.80	0.41	0.99
1-year-old	0.00	0.00	0.00	0.75	0.41	0.99
2-year-old	0.00	0.00	0.00	0.71	0.41	0.90
3-year-old	0.28	0.00	0.50	0.84	0.69	0.93
Adult	0.58	0.23	0.82	0.84	0.69	0.93

Objective 2. Impact of change in hunting survival on population growth for Virginia's hunted black bear population.

I used the stage-based Leslie matrix from Objective 1 to evaluate a change in hunting survival (which could be achieved by changing harvest season length, changing hunter effort, increased bag limits, etc.) of Virginia's hunted black bear population given current reproductive and survival estimates (Table 28).

Survival rates used in the Leslie matrix were assumed to equal 'hunting survival' because observed 'non-hunting survival (Chapter 1, Table 13) was 0.998 and 0.995 for adult and subadult females respectively, and therefore assumed to be 1.0. Annual survival is a product of hunting survival and non-hunting survival). To investigate the impact of change in harvest rate on population growth, I used the equation: harvest rate = 1.0 - hunting survival estimate. As with Objective 1, the sensitivity of growth rate was evaluated by changing hunting survival for one age category at a time, varying the rate by 0.05 increments at a time. For ease of interpretation, I graphed harvest rate instead of hunting survival according to above-mentioned equation.

Objective 3. Population projection with lower than observed survival rates

I wanted to investigate the impact of sporadic lower survival on population size over time. Sporadic decreases of hunting survival (i.e., increased harvest rate) could be caused by increased archery harvest due to low mast production (a hypothesis commonly mentioned by VDGIF personnel) or by better than average weather conditions during the hunting season increasing hunter effort.

This model used estimates of population size over time rather than growth rate change to illustrate population trends. The census date for population size was March 1st, which immediately follows cub reproduction during the months of January and February. I used the following equations to calculate the total population size in year t+1:

$$N_{c,t+1} = N_{a,t} * s_a * r_a + N_{3,t} * s_3 * r_3$$

$$N_{i,t+1} = N_{i-1,t} * s_{i-1}$$

$$N_{a,t+1} = N_{a,t} * s_a + N_{n,t} * s_3$$

$$Female bear = \begin{bmatrix} 0 & 0 & 0 & 0.275 & 0.575 \\ 0.80 & 0 & 0 & 0 & 0 \\ 0 & 0.75 & 0 & 0 & 0 \\ 0 & 0 & 0.71 & 0 & 0 \\ 0 & 0 & 0 & 0.84 & 0.84 \end{bmatrix} \begin{array}{c} reproduction / year \\ cubs \\ 1-year-old \\ 2-year-old \\ 3-year-old, adults \end{array}$$

Figure 9. Life-stage Leslie Matrix for female black bears in Virginia with average survival and reproductive estimates from data collected during 1994-1999 (Table 28).

$$N(total)_{t+1} = N_{c,t+1} + \sum N_{i,t+1} + N_{a,t+1}$$

where N = population size at March 1^{st}, s = annual survival rate, r = annual reproduction, c = cubs, a = adults, i = age class (1,2,3 -year-olds), and t = time.

Mast production in Virginia was classified as 'poor' in 1987 and 1997 (Martin 1996). To simulate a possible sporadic impact on survival, I used low survival values (Table 28) for all age classes in years t = 1 and t = 11 of a 15-year projection of population size. This exercise was designed to illustrate the impact if average survival is lower for some years, perhaps due to above mentioned lower mast production, higher hunter success rate in some year, etc. We did not include density-dependent effects in this projection as Taylor et al. (1994) suggested that bear mortality is not influenced by density-dependent effects if population size < 75% K. For our model, I assumed that Virginia's bear population is < 75% of K to avoid inclusion of density-dependent effects in the Matrix model. This assumption appears to be true for many areas of Virginia, where economic / cultural carrying capacity (i.e., tolerance of people for bears) seems to be far below ecological carrying capacity (D. Steffen, VDGIF, personal communication).

RESULTS

Objective 1. Sensitivity analysis of live-history parameters for female black bears in Virginia's hunted black bear population.

Population growth rate for Virginia's hunted black bear population (λ) equaled 0.73 (r = - 0.31) for survival and reproduction estimates of the lower 95% confidence bounds (Table 28), 1.04 (r = 0.04) for the estimated average survival and reproduction, and 1.26 (r = 0.23) for the upper edge of the 95% confidence interval of the estimates. Adult female reproduction and survival had the greatest impact on population growth rate (λ). Decreasing litter size for reproducing 3-year-old female black bears to 0 cubs / year did not decrease λ < 1.0 (i.e., decreasing population trend) if adult female reproduction was kept at 0.575 female cubs / year (Fig. 10). When litter size was reduced from 0.5 female offspring / year to 0 (i.e., reproductive failure) for adult females for a separate simulation, population growth changed from $\lambda = 1.02$ to 0.57. Changing litter size by 0.1 female offspring / year from 0.3 to 0.2 decreased λ by 0.04 for adult females and 0.01 for 3-year- old females. Changing female survival by 0.10 from 0.80 to 0.70 annual survival rate decreased λ by 0.05 for adults and 0.02 for the remaining age classes (Fig. 11). Changes to adult survival had the greatest effect on λ.

Objective 2. Impact of change in hunting survival on population growth for Virginia's hunted black bear population.

We assumed non-hunting survival to be 1.0 (from Chapter 1) and simulated change in harvest rate with the goal of stabilizing population growth of Virginia's hunted black bear population. Keeping current estimates of survival and reproduction constant for all other age classes, adult female survival had to be lowered from 0.84 to 0.77 (i.e., harvest rate = 0.23) to stabilize population growth (i.e., $\lambda = 1.0$, Fig. 12). If both adult and 3-year-old survival were lowered simultaneously, $\lambda = 1.0$ when annual harvest rate for both age classes was 0.21.

Objective 3. Population projection of Virginia's hunted black bear population with lower than observed survival rates

One goal of Virginia's Black Bear Management Plan was to stabilize population growth in certain regions of Virginia (e.g., Rockingham and Augusta counties, which encompass the northern study area of CABS). Current estimates of survival and reproduction result in a model population growth rate of $\lambda = 1.04$, or 4% annually. Population projection simulated an increase of $N_0 = 5{,}000$ bears (a hypothetical population starting point) to $N_{14} = 8{,}001$ bears (Fig. 13). In objective 2, we simulated that population growth would stabilize ($\lambda = 1.0$) if annual adult female survival equaled 0.77 (currently estimated at 0.84, Table 28) and 3-year-old female survival rate was 0.84 with all other survival and reproduction values constant as estimated (Figs. 12). Alternatively, both adult and 3-year-old female survival could equal 0.79 to stabilize the population (Fig. 13).

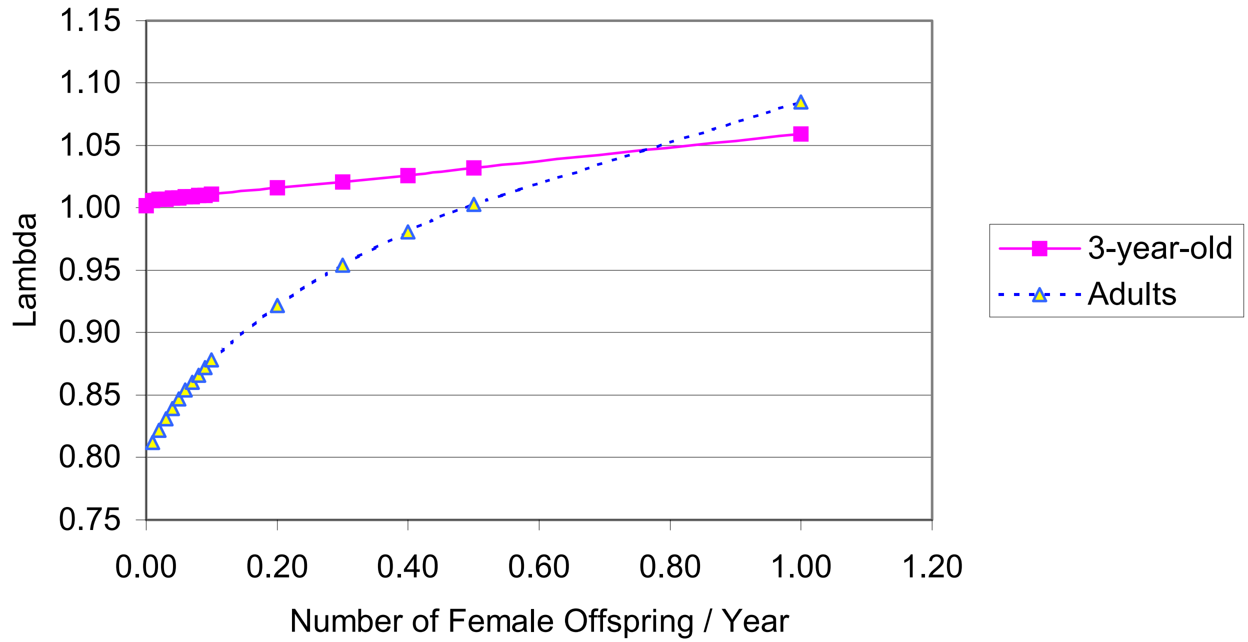

Figure 10. Sensitivity analysis for change in lambda (λ) with change in litter size for Virginia's hunted black bear population.

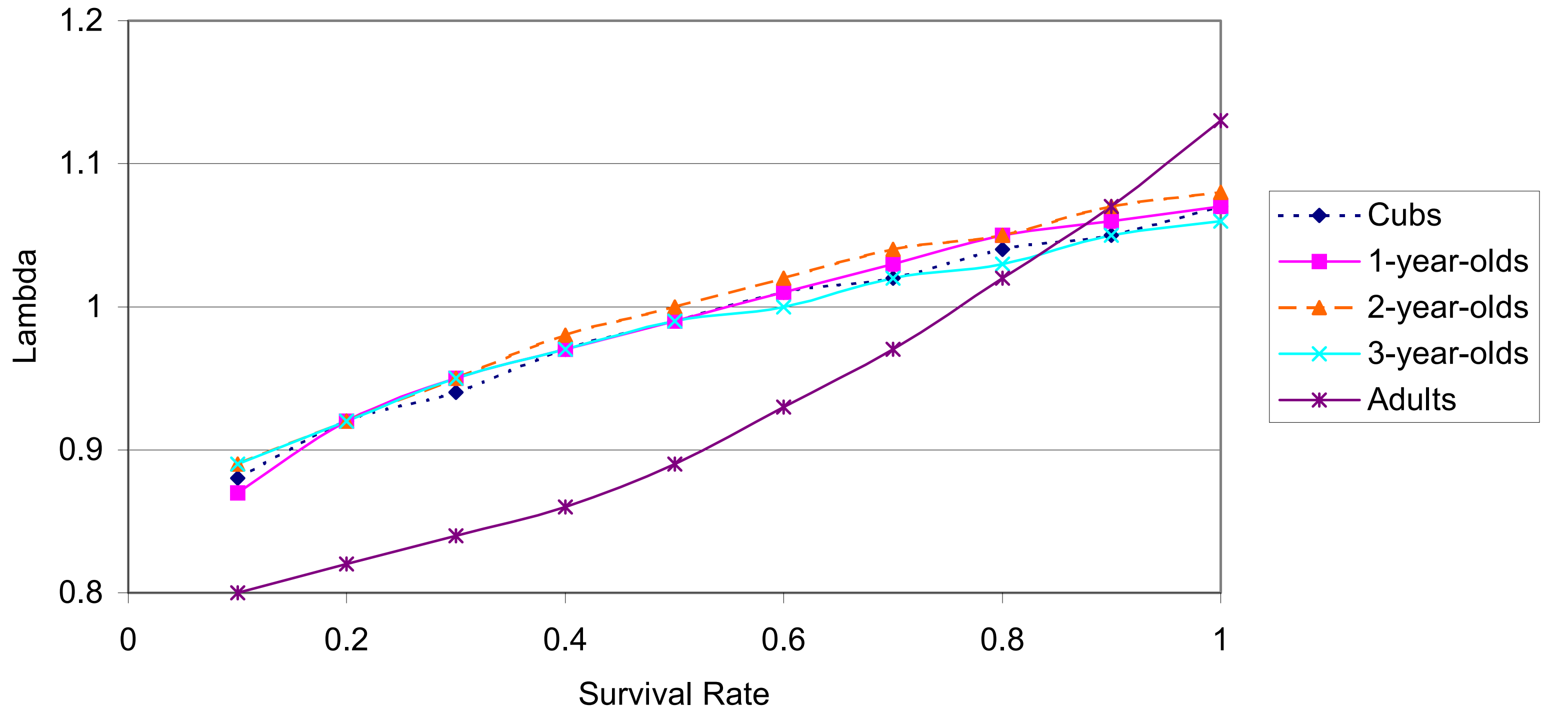

Figure 11. Sensitivity analysis for change in lambda (λ) with change in survival rate for Virginia's hunted black bear population.

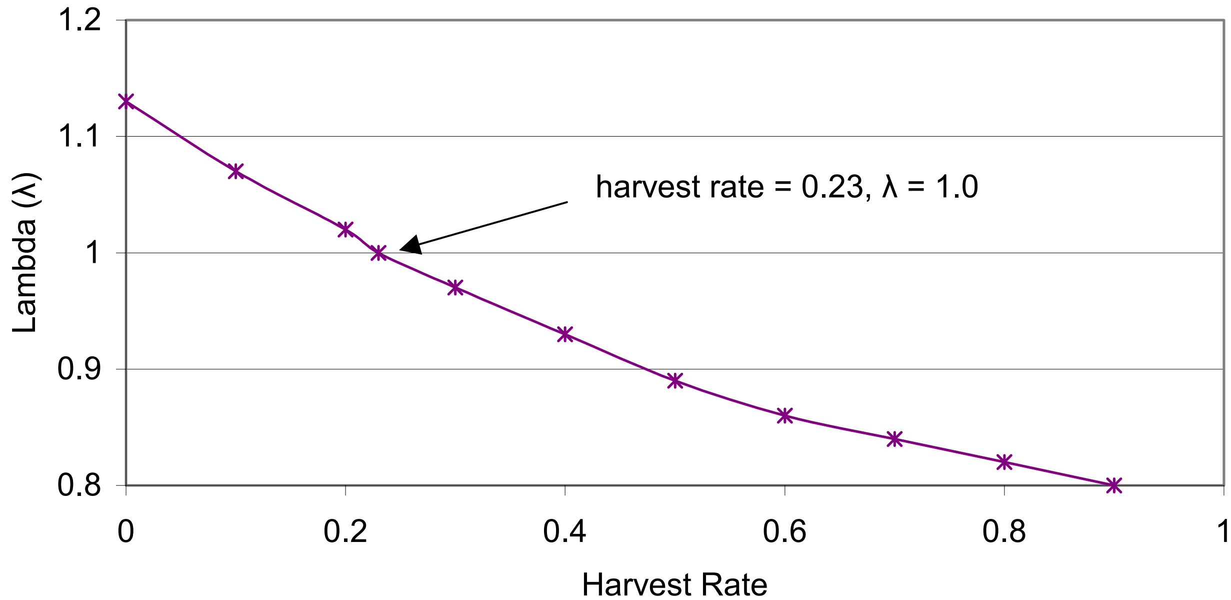

Figure 12. Harvest rate for adult females in relation to population growth rate (λ) for Virginia's hunted black bear population with current average survival and reproductive estimates for all other age classes.

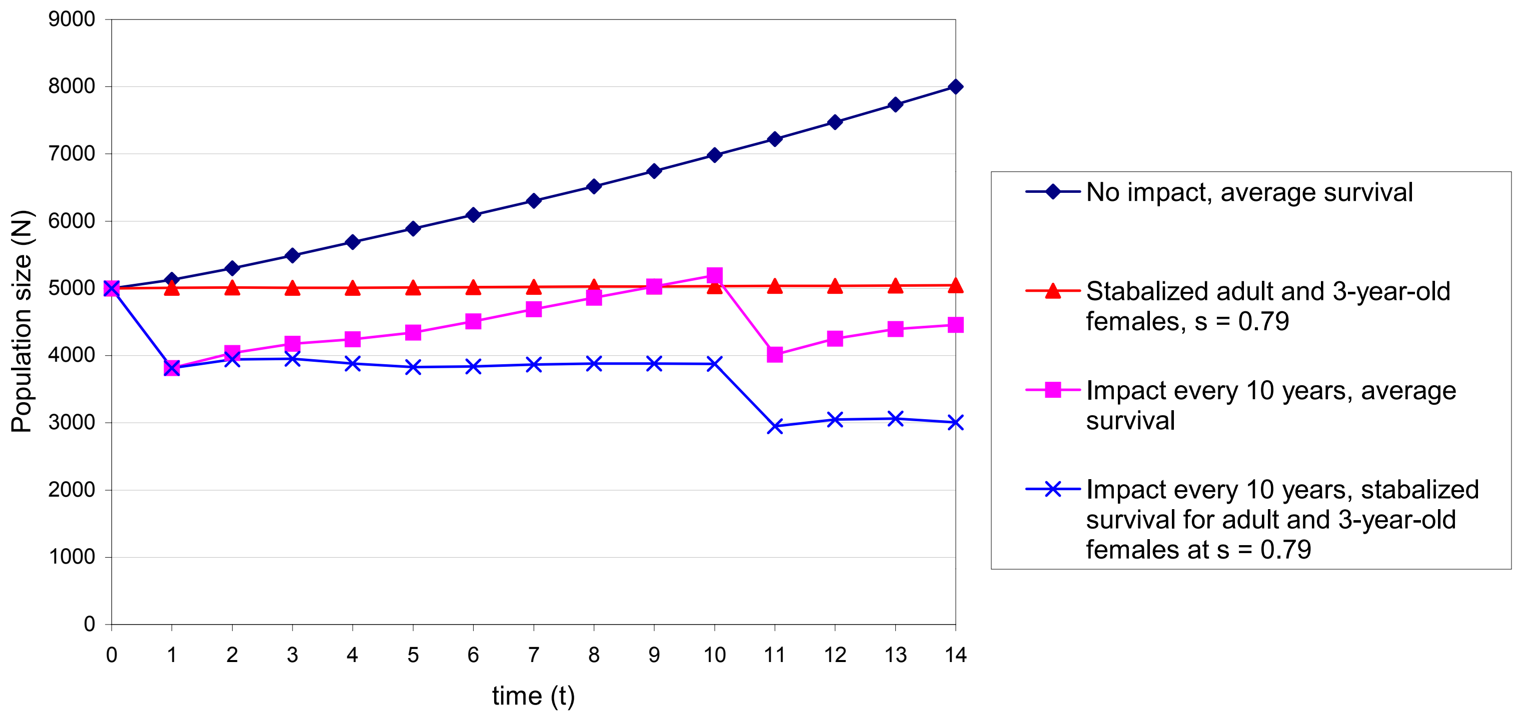

Figure 13. Population projections for Virginia's hunted black bear population with ranging values of survival and sporadic impact that lowers survival below estimated averages (s = annual survival rate; parameter values Table 28).

With only one event of lowered survival (0.69 for both 3-year-old and adult age categories and 0.41 for the remaining age categories; Table 28) and otherwise average survival as estimated by this study, it took the population 9 years to return to its original population size (Fig. 13). With 2 events of lowered survival at t = 1 and t = 11, population size fell from 5,000 at t = 0 to 4,457 at t = 14 (Fig. 13) for the 15-year period.

If adult and 3-year-old survival were 0.79 (value that would stabilize population growth with current survival estimates, see Objective 2), one event of lowered survival would not allow the population to return to its original population size but would stabilize at a lower level (Fig. 13). Each additional impact of lower survival would decrease the stable population size further. For example, lowered survival at times t = 1 and t = 11 would decrease population size from 5,000 at time t = 0 to 3,007 at t = 14 (Fig. 13).

DISCUSSION

Models are a simplified representation of reality that can aid in the understanding of a natural system, test hypotheses about that system, or make predictions (Bunnell and Tait 1980, Starfield and Bleloch 1986). Models are an abstract presentation of reality and should only include a minimal number of variables that still show the actual trend of a population (Starfield and Bleloch 1986). The addition of every possible parameter can complicate and confound the understanding of what causes changes in a population.

We chose a stage-based Leslie Matrix model to evaluate population dynamics of Virginia's hunted black bear population. Stage-based models are frequently used for long-lived species because data on specific ages are not available, demographic variables within age classes are not different, and individual age classes for a species that lives, for example, up to 30 years (like black bear), would result in matrixes of sizes up to 30 x 30 (Crouse et al. 1987, Manly 1990, Usher 1972). Stage-based matrix models are generally correctly displaying population trends, even if they are not precise in year-to-year variation (McLaughlin 1998, Starfield and Bleloch 1986). Since we only evaluated reproduction and survival in age categories (sample size for individual ages was too low), a stage-based rather than age-based matrix model was appropriate.

Modeling Virginia's hunted black bear population demonstrated the importance of adult female survival and continuous litter production for population growth. Black bears on the northern study area exhibited an average population growth rate of $\lambda = 1.04$, but which ranged from $\lambda = 0.73$ to $\lambda = 1.26$ for the 95% confidence bounds of our survival and reproduction estimates. Population growth in Shenandoah National Park during the 1980s was $\lambda = 1.0$ (Carney 1985), and only $\lambda = 1.0032$ for the Great Dismal Swamp (Hellgren 1988). Similarly, black bear population growth in Great Smoky Mountain National Park in Tennessee and North Carolina ranged from $\lambda = 1.0$ to 1.02 annually (McLean and Pelton 1994). The importance of the adult age class in population growth is influenced by higher reproduction of older age classes (Table 6), and the fact that it encompasses more animals (ages 4-30) rather than just one age class (age 3).

Virginia's black bear management plan (2001) identifies a need to stabilize population growth (i.e., keeping population size at current levels) for several western counties in Virginia, including Rockingham and Augusta where the northern study area of CABS is located. Currently, adult female black bears exhibit an annual survival rate of 0.84, which is assumed equal to hunting survival since non-hunting survival was 1.0 for radio-collared animals in the northern CABS study area between 1994-1999 (Chapter 1). Simulations showed that adult female survival could be lowered to 0.77 if all other age classes are kept at current estimates (or 0.79 if 3-year-old survival is lowered at the same time) to stabilize population growth rate from $\lambda = 1.04$ to $\lambda = 1.00$. This translates to a 31-44% increase in annual mortality for adult female black bears to stabilize population growth (to an annual mortality rate of 0.21-0.23).

However, if annual adult and 3-year-old female survival was lowered to 0.79 (possibly achieved by changes in hunting regulations, increased hunter effort or success, mast impact on survival or reproduction, etc.) to stabilize population growth, and survival is lower than average only once every 10 years, population size could decrease by 40% in 15 years (in simulation $N_0 = 5{,}000$, $N_{14} = 3{,}007$). This rapid response to increased adult mortality is common in long-lived mammals, which has been identified as the most important parameter in determining long-term population persistence (Emlen and Pikitch 1989). Managers have to be careful not to over-harvest a population, which could result in rapid population decline and slow recovery (McLean and Pelton 1994).

Reproductive failures due to lack of mast production have been observed in some states on the east coast (McLaughlin et al. 1994) and could affect Virginia when a mast failure is recorded. Kasbohm et al. (1996) did not find a difference in reproduction following the defoliation of oaks due to gypsy moth infestation and consequent oak mast failure in Shenandoah National Park. This situation differed from other mast failures, however, in that trees were defoliated, opening the canopy, and allowing soft mast species to grow. Complete reproductive failure in years of low mast production (like in Maine) has not been observed on this study. Future monitoring of reproduction during a complete mast failure (not observed during this study) might be an important factor in determining if reproduction changes during these events. If lowered reproduction is observed, the minimum annual survival rate (for adult and 3-year-old females) required to stabilize population growth could be above 0.79. If radio-collared females are not available for monitoring, instituting a mandatory submission of reproductive tracts might be an option to observe a change in litter production.

Simulations in this model used survival and reproduction estimates from the northern study area of CABS. If these scenarios for continued population growth are to be extrapolated to Virginia in general, it will be important to verify these parameters from other areas of the state where black bear populations might exhibit lower survival and reproductive parameters. Survival and reproductive estimates for the southern area were similar to our estimates for 1995 and 1996 data (Ryan 1997), but are based on only 2 years of data. In addition, Ryan (1997) calculated survival rates using the Kaplan-Meier estimator for data collected on radio-collared bears. Since we found a significant effect of radio-collars on black bear survival in the northern study area, I recommend analyzing data collected in the south using the summer captures and harvest returns to verify survival estimates. Since the model showed high sensitivity to change in adult females survival and reproduction, a re-evaluation of these parameters is necessary to apply this model to the southern study area.

CONCLUSIONS

The adult female black bear population on the northern study area of CABS can sustain a maximum of 23% average annual mortality given current estimates of survival and reproduction without decreasing current population levels. I caution that this is an average that must be adjusted with varying survival rates. This model does not include stochastic changes in survival and reproduction (such as change in weather during hunting season, mast production, etc) and only exhibits average trends. I recommend further investigation using a stochastic model to verify these simulations.

Population growth rate was most sensitive to changes in adult female survival and change of reproduction by adult females. Management efforts should focus on monitoring these parameters by keeping a certain number of females radio-collared and estimating survival periodically by marking bears during the summer and using harvest tag returns for a recapture sample during the winter. An effect of mast failure on reproduction has not been observed during this study, but should be carefully evaluated - especially after the 1999 ban of feeding on public lands (the effect of feeding on reproduction has not yet been established). To be applicable across Virginia, this model has to be verified with survival and reproductive estimates from other regions in Virginia.

CONCLUSIONS AND RECOMMENDATIONS

Black bears are a valuable environmental indicator due to their sensitivity to habitat alterations (Pelton and Beeman 1975). In the southeastern United States, the black bear has lost over 90% of its original range (Pelton 1986), persisting mostly in isolated islands of public land (Maehr 1984). Although Virginia's black bear population seems to be productive (large litter size: 2.35 cubs/litter, early age of reproduction: 3 years, and short breeding intervals: 2 years) and increasing ($\lambda = 1.04$), managers have to be careful not to over-harvest the population. Adult female survival and continuous reproduction (no lack of reproduction due to mast failures) were the most sensitive parameters to continued or stabilizing population growth. Simulations showed that increasing adult female mortality rate (harvest rate) from 0.16 to 0.23 could stabilize population growth ($\lambda = 1.0$) on the northern study area of CABS. Simulations also showed that the bear population can decrease rapidly if over harvesting adult females continues for only 1 harvest season.

To validate change in reproduction of adult females, VDGIF should consider keeping a number of adult females radio-collared to monitor reproduction in dens or alternatively, collecting reproductive tracts in an organized and continuous fashion. Reproductive tracts, however, will only show reproduction of the previous year since fetuses will not be detectable in reproductive tracts until mid to late December. Since we did not observe a complete mast failure during this study, it would be important to investigate if reproductive failure occurs during such an event. Estimating a change in survival rates could be accomplished by an intensive marking effort every 5 years and collecting tags at check stations to use in mark-dead recoveries estimates.

Survival estimates for black bears in Virginia were similar to other hunted black bear populations in North America. Adult females and adult males had annual survival rates of 0.84 and 0.77, respectively. The 3-year-old age class exhibited similar survival estimates to adults and ranged from 0.84 for females to 0.57 for males. Two-year old black bears exhibited the lowest survival rates ranging from 0.71 for females to 0.34 for males. Black bear density estimates on the northern study area ranged from 0.63 – 1.19 bears / km^2.

Survival estimates from radio-collard bears where biased high compared to the ear tagged sample. Hunters in Virginia might avoid harvesting radio-collared bears due to the belief that we mainly collar females. Survival estimates from tag returns and recaptures might be more reliable for a harvested population with hunter selectivity. Estimates from tag return might be even more improved if tags were collected at check stations rather than returned by hunters. Since bear hunters in Virginia already have to submit a tooth when they check the animal, it would not be too much effort to collect the tag in addition. Ear-tag numbers are usually recorded at the check stations, but if collected could reduce recording error even further and maybe improve estimates.

Monitoring black bears in Virginia might be achieved by combining several indices, including the bait station index (best at this point), archery harvest, and vehicle collision data. These indices might not show an annual variation in proportion to actual population increase or decrease, but should detect a change in population trend if conducted over several years.

Before extrapolating our findings to the state of Virginia, I recommend validating these findings with the southern study area. The southern area of CABS should be the focus of attention in the last 3 years of this study to improve the existing data set for this area with more and reliable estimates. Currently, we are missing good population density estimates and survival data (especially monitoring data for estimates on radio-collared bears) in that area that could be used for comparing survival rate between radio-collared and ear tagged bears.

A careful monitoring program is important in the future because bears can be over-harvested easily and will take years to recover.

LITERATURE CITED

Abler, W. A. 1988. Evaluation of sardine bait stations for indexing black bears in southeast Georgia. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 42:396-403.

Alt, G. L. 1981. Reproductive biology of black bears in northern Pennsylvania. Transactions of the Northeastern Fisheries and Wildlife Conference 38:88-89.

Alt, G. L. 1982. Reproductive biology of Pennsylvania's black bear. Pennsylvania Game News 53:9-15.

Alt, G. L. 1989. Reproductive biology of female black bears and early growth and development of cubs in northeastern Pennsylvania. Dissertation. West Virginia University. Morgantown, WV, USA. 187 pp.

Alt, G. L., G. L. Matula, Jr., F. W. Alt, and J. S. Lindzey. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. International Conference on Bear Research and Management 4:131-136.

Anderson, D. R., K. P. Burnham, W. R. Gould, and S. Cherry. 2001. Concerns about finding effects that are actually spurious. Wildlife Society Bulletin 29:311-316.

Anderson, D. R., K. P. Burnham, and G. C. White. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. Journal of Animal Ecology 54:89-98.

Anderson, D. R., M. A. Wotawa, and E. A. Rexstad. 1993. Trends in the analysis of recovery and recapture data. Pages 73-98 *in* Lebreton, J.D., and P.M. North, editors. Marked Individuals in the Study of Bird Populations. Birkhauser Verlag. Berlin, Germany.

Bartmann, R. M., G. C. White, L. H. Carpenter, and R. A. Garriot. 1987. Aerial mark-recapture estimates of confined mule deer in Pinyon-Juniper woodland. Journal of Wildlife Management 51:41-46.

Beck, T. D. I. 1991. Black bears of west-central Colorado. State of Colorado Division of Wildlife. Fort Collins, CO. 86 pp.

Beecham, J. J. 1983a. Population characteristics of black bears (*Ursus americanus*) in west central Idaho, (USA). Journal of Wildlife Management 47:405-412.

Beecham, J. J. 1983b. Timing of parturition of black bears (*Ursus americanus*) in northeastern Pennsylvania. Journal of Mammalogy 24:305-307.

Beeman, L. E., and M. R. Pelton. 1980. Seasonal food habits and feeding ecology of black bears in the Smoky Mountains. International Conference on Bear Research and Management 4:141-147.

Bowden, D. C., and R. C. Kufeld. 1995. Generalized mark-resight population size estimation applied to Colorado moose. Journal of Wildlife Management 59:840-851.

Buckland, S. T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. Biometrics 36:419-435.

Bunnell, F. L., and D. E. N. Tait. 1980. Bears in models and in reality-implications to management. International Conference on Bear Research and Management 4:201-204.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic 38:316-323.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199-213 *in* Lebreton, J.-D., and P.M. North, editors. Marked individuals in the study of bird population. Birkhauser Verlag. Basel, Switzerland.

Burnham, K. P., and D. R. Anderson. 1998. Model Selection and Inference: A practical information-theoretic approach. Springer Verlag. New York, USA.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection in the analysis of capture-recapture data. Biometrics 51:888-898.

Burton, T., D. Koch, D. Updike, and A. Brody. 1994. Evaluation of the potential effects of sport hunting on California black bears. International Conference on Bear Research and Management 9:231-236.

Carlock, D. M., R. H. Conley, J. M. Collins, P. E. Hale, K. G. Johnson, A. S. Johnson, and M. R. Pelton. 1983. The Tri-State Black Bear Study. Pope and Young Club. Knoxville, TN.

Carney, D. W. 1985. Population dynamics and denning ecology of black bears in Shenandoah National Park, Virginia. M.S. thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA. 89 pp.

Catchpole, E. A., S. N. Freeman, and B. J. T. Morgan. 1995. Modeling age variation in survival and reporting rates for recovery models. Journal of Applied Statistics 22:597-609.

Caughley, G. 1977. Analysis of vertebrate populations. The Pitman Press. Bath, United Kingdom.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publication in Statistics 1:131-160.

Chatfield, C. 1995. Model uncertainty, data mining and statistical inference. Journal of the Royal Statistical Society 158:419-466.

Clark, J. D., and K. G. Smith. 1994. A demographic comparison of two black bear populations in the Interior Highlands of Arkansas. Wildlife Society Bulletin 22:593-603.

Coggin, J. L., and C. H. Peery. 1971. A system for evaluating the oak mast crop. Virginia Department of Game and Inland Fisheries. Verona, VA.

Comly, L. M. 1993. Survival, reproduction, and movements of translocated nuisance black bears in Virginia. M.S. thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA. 113 pp.

Comly, L. M., and M. R. Vaughan. 1997. Survival and reproduction of translocated Virginia black bears. International Conference on Bear Research and Management 9:113-117.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412-1423.

Cutler, T. L., and D. E. Swann. 1999. Using remote photography in wildlife ecology: a review. Wildlife Society Bulletin 27:571-581.

Davis, D. E., and R. L. Windstead. 1980. Estimating the numbers of wildlife populations. Pages 221-245 *in* Schemnitz, S.D., editor. Wildlife Management Techniques Manual. 4th edition. The Wildlife Society. Washington, D.C, USA.

Dice, L. R. 1941. Methods for estimating populations of mammals. Journal of Wildlife Management 5:398-407.

Eberhardt, L. L. 1990. Survival rates required to sustain bear populations. Journal of Wildlife Management 54:587-590.

Eiler, J. H., W. G. Wathen, and M. R. Pelton. 1989. Reproduction in black bears in the southern Appalachian mountains (USA). Journal of Wildlife Management 53:353-360.

Elowe, K. D., and W. E. Dodge. 1989. Factors affecting black bear reproductive success and cub survival. Journal of Wildlife Management 53:962-968.

Emlen, J. M., and E. K. Pikitch. 1989. Animal population dynamics: identification of critical components. Ecological Modeling 44:253-273.

Garner, N. P. 1986. Seasonal movements, habitat selection, and food habits of black bears (*Ursus americanus*) in Shenandoah National Park. M.S. Thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA. 104 pp.

Garshelis, D. L. Nuisance bear activity and management in Minnesota. 1989. Pages 169-180 *in*, Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada.

Garshelis, D. L. 1990. Monitoring effects of harvest on black bear populations in North America: a review and evaluation of techniques. Eastern Workshop on Black Bear Research and Management 10:120-144.

Garshelis, D. L. 1991. Mark-recapture estimation for animals with large home ranges. Pages 1098-1111 *in* McCullough, D.R., and R.H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science. London, UK.

Garshelis, D. L. 1992. Estimating bear population size. Pages 1098-1111 *in* McCullough, D.R., and R.H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science. London, UK.

Garshelis, D. L. 1993. Monitoring black bear populations: pitfalls and recommendations. Proceedings of the Fourth Western Black Bear Workshop:123-144.

Garshelis, D. L., and E. C. Hellgren. 1994. Variation in reproductive biology of male black bears. Journal of Mammalogy 75:175-188.

Garshelis, D. L., and L. G. Visser. 1997. Enumerating megapopulations of wild bears with an ingested biomarker. Journal of Wildlife Management 61:466-480.

Gese, E. M. 2000. Monitoring of terrestrial carnivore populations. Pages 373-396 *in* J.L. Gittleman, S.M.L. Funk, and D. MacDonald, editors. Carnivore Conservation. Cambridge University Press. Cambridge, UK.

Gibbs, J. P. 2000. Monitoring populations. Pages 213-252 *in* Boitani, L., and T.K. Fuller, editors. Research techniques in animal ecology - controversies and consequences. Columbia University Press. New York, N.Y.

Godfrey, C. L. 1996. Reproductive biology and denning ecology of Virginia's exploited black bear population. M.S. thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA.

Gotelli, N. J. 1998. A primer of ecology. Sinauer Associates, Inc. Sunderland, MA.

Gross, J. E. 1972. Criteria for big game planning: performance measures vs. intuition. Transactions of the North American Wildlife and Natural Resources Conference 37:246-258.

Harlow, R. F. 1961. Characteristics and status of Florida black bear. Transactions of the North American Wildlife Conference 26:481-495.

Harris, R. B., L. H. Metzgar, and C. D. Bevins. 1986. GAPPS, Generalized animal population projections system, user's manual. Montana Cooperative Wildlife Research Unit, University of Montana. Missoula, MT. 123 pp.

Hayne, D. W. 1984. Population dynamics and analysis. Pages 203-210 *in* Halls, L.W., editor. White-tailed deer ecology and management. Stackpole Books. Harrisburg, PA.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using radio telemetry. Journal of Wildlife Management 49:668-674.

Hellgren, E. C. 1988. Ecology and physiology of a black bear (*Ursus americanus*) population in Great Dismal Swamp and reproductive physiology in the captive female black bear Ph. D. Dissertation. Virginia Polytechnic Institute and State University. Blacksburg, VA. 231 pp.

Hellgren, E. C., D. W. Carney, N. P. Garner, and M. R. Vaughan. 1988. Use of breakaway cotton spacers on radio collars. Wildlife Society Bulletin 16:216-218.

Hellgren, E. C., and M. R. Vaughan. 1989a. Demographic analysis of a black bear population in the Great Dismal Swamp (Virginia, North Carolina, USA). Journal of Wildlife Management 53:969-977.

Hellgren, E. C., and M. R. Vaughan. 1989b. Rectal temperatures of immobilized, snare-trapped black bears in Great Dismal Swamp. Journal of Wildlife Diseases 25:440-443.

Herrero, S. 1985. Bear attacks : their causes and avoidance. Nick Lyons Books/Winchester Press. New York, NY. 287 p.

Higgins, J. C. 1997a. Survival, home range, and spatial relationships of Virginia's exploited black bear population M. S. Thesis. Virginia Polytechnic Institute and State University. Blacksburg. 124 pp.

Higgins, K. L. 1997b. Hunting Dynamics, condition estimates, and movement of black bears hunted with hounds in Virginia M. S. Thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA.

Holling, C. S. 1978. Adaptive environmental assessment and management. Wiley. Chichester, UK.

Johnson, D. R., N. C. Nydegger, and G. W. Smith. 1987. Comparison of movement-based density estimates for Townsend ground squirrels in southwestern Idaho. Journal of Mammalogy 68:689-691.

Johnson, K. G. 1992. Bait-station surveys to monitor relative density, distribution, and activities of black bears in the southern Appalachian region. University of Tennessee. Knoxville, TN.

Jonkel, C. J., and I. M. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27:57pp.

Kane, D. M., and J. A. Litvaitis. 1992. Age and sex composition of live-captured and hunter-killed samples of black bears. Journal of Mammalogy 73:215-217.

Kaplan, E. L., and P. Meier. 1958. Nonparametric estimation from incomplete observations. Journal of the American Statistical Association 53:457-481.

Karanth, K. U. 1995. Estimating tiger (*Panthera tigris*) populations from camera-trap data using capture-recapture models. Biological Conservation 71:333-338.

Kasbohm, J. W. 1994. Response of black bears to gypsy moth infestation in Shenandoah National Park, Virginia. Ph. D. Thesis. Virginia Polytechnic Institute and State University, Blacksburg. Blacksburg, VA. 217 pp.

Kasbohm, J. W., M. R. Vaughan, and J. G. Kraus. 1996. Effects of gypsy moth infestation on black bear reproduction and survival. Journal of Wildlife Management 60:408-416.

Kasworm, W. F., and J. T. Their. 1994. Adult black bear reproduction, survival and mortality sources in northwest Montana. International Conference on Bear Research and Management 9:223-230.

Keay, J. A. 1995. Black bear reproductive rates in Yosemite National Park. California Fish and Game 81:122-131.

Kleinbaum, D. G., and L. L. Kupper. 1978. Applied regression analysis and other multivariate methods. Duxbury Press. Boston, MA, USA.

Knight, R. R., and L. L. Eberhardt. 1984. Projected future abundance of the Yellowstone grizzly bear. Journal of Wildlife Management 48:1434-1438.

Koch, D. B. 1994. Biopolitical management of mountain lions, tule elk, and black bears in California. International Conference on Bear Research and Management 9:561-566.

Kohn, B. E. 1982. Status and management of black bears in Wisconsin. Wisconsin Department of Natural Resources. Report 129. Madison, WI.

Kolenosky, G. B. 1986. The effects of hunting on an Ontario black bear population. International Conference on Bear Research and Management 6:45-55.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference on Bear Research and Management 7:305-316.

Kozak, S. J. 1970. Geology of the Elliot Knob, Deerfield, Craigsville, and Augusta Springs Quadrangle, VA. Virginia Division of Mineral Resources. Report 21.

Kucera, T. E., and R. H. Barrett. 1993. The trailmaster camera system for detecting wildlife. Wildlife Society Bulletin 21:505-508.

Lancia, R. A., J. D. Nichols, and K. H. Pollock. 1994. Estimating the number of animals in wildlife populations. *in* Bookhout, T.A., editor. Research and Management Techniques for Wildlife and Habitats. 5th edition. The Wildlife Society. Bethesda, MD, USA.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

LeCount, A. L. 1982. Characteristics of a central Arizona black bear (*Ursus americanus*) population. Journal of Wildlife Management 46:861-868.

LeCount, A. L. 1983. Evidence of wild black bears breeding while raising cubs. Journal of Wildlife Management 47:264-268.

LeCount, A. L. 1987. Causes of black bear cub mortality. International Conference on Bear Research and Management 7:75-82.

Lincoln, F. C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular of the U.S. Department of Agriculture 118:1-4.

Lint, R. J., B. D. Leopold, and G. A. Hurst. 1995. Comparison of abundance indices and population estimates for wild turkey gobblers. Wildlife Society Bulletin 23:164-168.

Liu, X., and Q. Xiano. 1986. Age composition, sex ratio and reproduction of bears in Heilongjiang Province, China. Acta Theriologica Sinica 6:161-170.

Loker, C. A., and D. J. Decker. 1995. Colorado black bear hunting referendum: what was behind the vote? Wildlife Society Bulletin 23:370-376.

Maehr, D. S. 1984. Distribution of black bears in eastern North America. Proceedings of the Eastern Workshop on Black Bear Management and Research 7:74.

Manly, B. F. J. 1990. Stage-structured populations. Chapman and Hall. London, UK.

Martin, D. D. 1996. Virginia Mast Status Report. Virginia Department of Game and Inland Fisheries. Verona, VA.

Martin, D. D., and D. Steffen. 2000. Virginia black bear status report. Virginia Wildlife Resource Bulletin 8:1-33.

Martorello, D. A., T. H. Eason, and M. R. Pelton. 2001. A sighting technique using cameras to estimate population size of black bears. Wildlife Society Bulletin 29:560-567.

Matthews, S. J. K. 1977. The seasonal, altitudinal, and vegetational incidences of black bear scats in the Great Smoky Mountain National Park. M.S. Thesis. University of Tennessee. Knoxville, TN.

McCullough, D. R. 1979. The George Reserve deer herd - population ecology of a K - selected species. University of Michigan Press. Ann Arbor, MI, USA. 271 p.

McCullough, D. R., and D. H. Hirth. 1988. Evaluation of the Petersen-Lincoln estimator for a white-tailed deer population. Journal of Wildlife Management 52:534-544.

McLaughlin, C. R. 1998. Modeling effects of food and harvests on female black bear populations Ph.D. Dissertation. University of Maine. MA. 263 pp.

McLaughlin, C. R., G. J. Matula, and R. L. O'Connor. 1994. Synchronous reproduction in Maine black bears. International Conference on Bear Research and Management 9:471-479.

McLean, P. K., and M. R. Pelton. 1994. Estimates of population density and growth of black bears in the Smoky Mountains. International Conference on Bear Research and Management 9:253-261.

McLellan, B. N. 1989. Dynamics of a grizzly bear population during a period of industrial resource extraction. Canadian Journal of Zoology 67:1856-1860.

Menkens, G. E. J., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69:1952-1959.

Miller, D. A. 1993. Preliminary investigation into bait station use to monitor black bear populations in Mississippi. M. S. Thesis. Mississippi State University. MS.

Miller, S. D. 1990. Population management of bears in North America. International Conference on Bear Research and Management 8:357-373.

Miller, S. D., E. F. Becher, and W. B. Ballard. 1987. Black and brown bear density estimates using modified capture-recapture techniques in Alaska. International Conference of Bear Research and Management 7:23-35.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, Jr., R. B. Smith, R. R. Nelson, W. B. Ballard, and C. C. Schwartz. 1997. Brown and black bear density estimation in Alaska using radio telemetry and replicated mark-resight techniques. Wildlife Monographs 133:1-55.

Minta, S., and M. Mangel. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. Ecology 70:1738-1751.

Mowat, G., and C. Strobeck. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. Journal of Wildlife Management 64:183-193.

Neal, A. K., G. C. White, R. B. Gill, D. F. Reed, and J. H. Olterman. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. Journal of Wildlife Management 57:436-450.

Needham-Echols, K. 2000. Aspects of reproduction and cub survival in a hunted population of Virginia black bears M.S. Virginia Polytechnic Institute and State University. Blacksburg. 101 pp.

Noyce, K. V., and D. L. Garshelis. 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. International Conference on Bear Research and Management 9:481-496.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62:1-135.

Pelton, M. R. 1982. Black Bear. *in* Chapman, J.S., and G.A. Feldhamer, editors. Wild Mammals of North America - Biology, Management, and Economics. Johns Hopkins University Press. Baltimore, MD.

Pelton, M. R. 1986. Habitat needs of black bears in the East. *in* Kulhany, D.L., and R.N. Conner, editors. Wilderness and natural areas in the Eastern United States: a management challenge. Center for Applied Studies, Stephen F. Austin State University. Nacogdoches, TX.

Pelton, M. R., and L. E. Beeman. A synopsis of population studies of the black bear in the Great Smoky Mountains National Park. 1975. Pages 43-48 *in* Southern Regional Zoo Workshop, American Association of Zoological Parks and Aquariums, Knoxville, TN.

Pelton, M. R., and L. C. Marcum. The potential use of radio-isotopes for determining densities of black bears and other carnivores. 1977. Pages 221-237 *in* Phillips, R.L., and C. Jonkel editors, University of Montana, Montana Forest Conservation Experimental Station.

Pelton, M. R., and F. T. Van Manen. 1996. Benefits and pitfalls of long-term research: A case study of black bears in Great Smoky Mountains National Park. Wildlife Society Bulletin 24:443-450.

Petersen, C. G. J. 1896. The yearly immigration of young plaice into the Limfjord from the German Sea. Report of the Danish Biological Station 6:1-48.

Pharris, L. D. 1981. Evaluation of black bear survey data in Arkansas, 1976-1980. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 35:66-70.

Pojar, T. M. 1981. A management perspective of population modeling. Pages 241-261 *in* Fowler, C.W., and T.D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons. New York, N.Y.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752-757.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107:1-77.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. Journal of Wildlife Management 53:7-15.

Rawinski, T. J., G.P. Fleming, and F. V. Judge. 1994. Forest vegetation of the Ramsey's Draft and Little Laurel Rung Research Natural Areas, Virginia: baseline ecological monitoring and classification. Virginia Department of Conservation and Recreation, Division of Natural Heritage. Report 94-14. Richmond, VA.

Reynolds, D. G., and J. J. Beecham. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference on Bear Research and Management 4:181-190.

Rogers, L. 1976a. Social relationships, movements, and populations dynamics of black bears in northeastern Minnesota. Ph.D. University of Minnesota. Minneapolis. 194 pp.

Rogers, L. L. 1976b. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. Transactions of the North American Wildlife and Natural Resources Conference 41:431-438.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota (USA). Wildlife Monographs 97:1-72.

Romin, L. A., and J. A. Bissonette. 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24:276-283.

Roseberry, J. L., and A. Woolf. 1991. A comparative evaluation of techniques for analyzing white-tailed deer harvest data. Wildlife Monographs 117:1-59.

Ryan, C. W. 1997. Reproduction, survival, and denning ecology of black bears in southwestern Virginia. M.S. Virginia Polytechnic Institute and State University. Blacksburg. 124 pp.

Samson, C., and J. Huot. 1995. Reproductive biology of female black bears in relation to body mass in early winter. Journal of Mammalogy 76:68-77.

Schnabel, Z. E. 1938. Estimation of the size of animal populations by marking experiments. U.S. Fish and Wildlife Service Fisheries Bulletin 69:191-203.

Schrage, M. W. 1994. Influence of gypsy moth induced oak mortality on a black bear population. M.S. thesis. Virginia Polytechnic Institute and State University. Blacksburg, VA. 113 pp.

Schwartz, C. C., and A. W. Franzmann. 1991. Interrelationship of black bears to moose and forest succession in the northern coniferous forest. Wildlife Monographs 113:1-58.

Schwartz, C. C., and A. W. Franzmann. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. Journal of Wildlife Management 56:426-431.

Seber, G. A. F. 1982. The estimation of animal abundance. MacMillan Publishing Company. New York, N.Y.

Seber, G. A. F. 1986. A review of estimating animal abundance. Biometrics 42:267-292.

Seguin, R. J. 1992. Possible simultaneous rearing of consecutive litters by black bears. Canadian Field Naturalist 106:514-516.

Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. International Conference on Bear Research and Management 5:133-139.

Smith, T. R. 1985. Ecology of black bears in a bottomland hardwood forest of Arkansas. Ph.D. Dissertation. University of Tennessee. Knoxville, TN.

Soil Conservation Service. 1985. Soil survey of Giles County, Virginia, southern and central parts. Soil Conservation Service, USDA. Washington, D.C.

Starfield, A. M., and A. L. Bleloch. 1986. Building models for conservation and wildlife management. Macmillan Publishing Company. New York. 253 p.

Strickley, A. R., Jr. 1961. A black bear tagging study in Virginia. Proceedings of the Annual Conference of Southeast Association of Game and Fish Commissions 15:43-54.

Taylor, M. K., D. P. Demaster, F. L. Bunnell, and R. E. Schweinsburg. 1987. Modeling the sustainable harvest of female polar bears. Journal of Wildlife Management 51:811-820.

Trent, T. T., and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. Journal of Wildlife Management 38:459-472.

Usher, M. B. 1972. Developments in the Leslie Matrix Model. *in* Jeffers, J.N.R., editor. Mathematical models in ecology. Blackwell Scientific Publications. Oxford, UK.

van Manen, F. T., J. D. Clark, T. H. Eason, and M. R. Pelton. unpublished manuscript. An evaluation of bait-station surveys as an index of black bear population abundance. Ursus.

Vangilder, L. D., and S. L. Sheriff. 1990. Survival estimation when fates of some animals are unknown. Transactions of the Missouri Academy of Science 24:57-65.

Vaughan, M. R., P. F. Scanlon, S. P. Mersmann, and D. D. Martin. 1990. Black bear damage in Virginia. Fourth Eastern Wildlife Damage Control Conference 4:147-154.

Wathen, W. G. 1983. Reproduction and denning of black bears in the Great Smoky Mountains. M.S. thesis. University of Tennessee. Knoxville, TN.

White, G. C. 1996. NOREMARK: Population estimation from mark-resight surveys. Wildlife Society Bulletin 24:50-52.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory. Report LA-8787-NERP. 235 pp.

White, G. C., and K. P. Burnham. 1995. Program MARK: survival estimation from populations of marked animals (online). http://www.cnr.colostate.edu.FWB/.

White, G.C, and Shenk, T.M. unpublished manuscript. Population estimation with radio-marked animals.

Willey, C. H. 1974. Aging black bears from first premolar tooth sections. Journal of Wildlife Management 38:97-100.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of a nested grid approach for estimating density. Journal of Wildlife Management 49:675-678.

Wright, B. A. 1989. Virginia Wildlife - related recreation study. Virginia Department of Game and Inland Fisheries. Manassas, VA.

Wright, B. A., N.D. Emerald, C. Cox, M. Thomas, D.E. Steffen. 2000. Virginia survey of hunter harvest, effort, and attitudes 1998-1999. Center for Recreation Resources Policy, George Mason University. Manassas, VA. 67 pp.

Young, B. F., and R. L. Ruff. 1982. Population dynamics and movements of black bears (*Ursus americanus*) in east central Alberta. Journal of Wildlife Management 46:845-860.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12:163-169.

APPENDICES

Appendix 1. Trapping totals by year and trap success rate for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Year	Number of captures	Number of trapnights	Capture / trapnight	Success rate (%)
1994	134	2,152	16.1	6.2
1995	122	1,877	15.4	6.5
1996	138	1,427	10.3	9.7
1997	157	1,115	7.1	14.1
1998	149	1,170	7.9	12.7
1999	174	1,091	6.3	15.9
2000	134	1,280	9.6	10.5
Total	1,008	10,112	10.0	10.0

Appendix 2. Number of radio-collared black bears monitored between 1994-1999 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia.

Year	Females	Males	Sex ratio (M:F)
1994	32	11	1:2.9
1995	60	11	1:5.5
1996	60	7	1:8.6
1997	51	12	1:4.3
1998	44	17	1:2.6
1999	64	12	1:5.3
2000	58	9	1:6.4

Appendix 3. Annual survival rates for subadult male black bears radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Heisey and Fuller 1989).

Year	Number of radio days	N	Number of deaths	Survival estimate	95% C.I.
1994	851	7	0	1.000	1.000 - 1.000
1995	1,158	5	3	0.442	0.175 - 1.000
1996[a]	--	0	--	--	--
1997	595	4	3	0.320	0.087 - 1.000
1998	504	4	2	0.456	0.154 - 1.000
1999	572	4	1	0.532	0.155 - 1.000
2000	371	1	0	1.000	1.000 - 1.000
Geometric Mean				0.570	0.267 – 1.000

[a] no subadult males were radio-collared in 1996.

Appendix 4. Annual survival rates for subadult female black bears radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Heisey and Fuller 1989).

Year	Number of radio days	N	Number of deaths	Survival estimate	95% C.I.
1994	1,606	11	1	0.863	0.641 - 1.000
1995	2,170	16	0	1.000	1.000 - 1.000
1996	1,667	14	0	1.000	1.000 - 1.000
1997	1,689	8	0	1.000	1.000 - 1.000
1998	264	6	0	1.000	1.000 - 1.000
1999	1,767	12	0	1.000	1.000 - 1.000
2000	3,014	11	1	0.876	0.676 - 1.000
Geometric Mean				0.961	0.887 – 1.000

Appendix 5. Annual survival rates for adult male black bears radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Heisey and Fuller 1989).

Year	Number of radio days	N	Number of deaths	Survival estimate	95% C.I.
1994	489	4	0	1.000	1.000 - 1.000
1995	956	6	0	1.000	1.000 - 1.000
1996	1,497	7	1	0.595	0.215 - 1.000
1997	1,582	8	1	0.866	0.653 - 1.000
1998	2,119	13	2	0.455	0.153 - 1.000
1999	1,415	8	2	0.684	0.402 - 1.000
2000	1,970	8	2	0.697	0.421 - 1.000
Geometric Mean				0.731	0.448 – 1.000

Appendix 6. Annual survival rates for adult female black bears radio-collared between 1994-2000 for the Cooperative Alleghany Bear Study Northwest, George Washington and Jefferson National Forests, Virginia (Heisey and Fuller 1989).

Year	Number of radio days	N	Number of deaths	Survival estimate	95% C.I.
1994	3,129	21	2	0.877	0.727 - 1.000
1995	10,014	44	1	0.972	0.918 - 1.000
1996	13,012	46	1	0.973	0.923 - 1.000
1997	13,049	43	7	0.814	0.699 - 0.948
1998	11,622	38	3	0.909	0.817 - 1.000
1999	13,217	52	3	0.925	0.848 - 1.000
2000	12,209	47	0	1.000	1.000 - 1.000
Geometric Mean				0.922	0.841 –0.992

Appendix 7. Population estimates using a Lincoln-Petersen estimate with Chapman's (1951) modification for the entire area of the northwest study area of the Cooperative Alleghany Bear Study for the summers 1998 – 2000 on the George Washington and Jefferson National Forests, Virginia.

Year	Sex	Marked bears	Marked bears recaptured	Unmarked bears observed	Population estimate	95% C.I.	Adjusted population estimate	Bears / km^2	Marking period end
1994	Both	41	8	38	218	109	109-328	0.21	30-Jul
1995	Both	50	4	46	519	376	143-895	0.51	22-Jul
1996	Both	56	18	48	200	61	139-261	0.20	14-Jul
1997	Both	60	11	56	345	153	192-498	0.34	9-Jul
1998	Both	57	14	53	262	98	164-360	0.26	11-Jul
1999	Both	68	14	67	376	148	228-524	0.39	17-Jul
1994	M	32	6	27	159	88	71-247		19-Jul
1995	M	33	3	27	263	203	60-466		22-Jul
1994	F	9	1	12	69	66	3-135		31-Jul
1995	F	18	0	19	--	--	--		19-Jul

Appendix 8. Parameter values used in monitoring index correlations (Chapter 3). Dead return population estimate calculated in Chapter 2 (Table 20). All other data provided by VDIGIF.

Year	% baits hit	Auto accidents	Mast index	Archery harvest	Non-dog harvest	Dog harvest	Total harvest	Dead return population estimates	Damage complaints
1994		29	18.5	89	152	278	517	584	64
1995	11.5	28	25.6	81	205	316	602	505	98
1996	12.5	22	20.5	56	172	395	624	471	62
1997	22.0	31	7.2	222	271	295	788	803	127
1998	13.8	20	17.1	110	337	467	914	488	108
1999	29.5	--	18.8	228	246	432	915	882	--

VITA

Sybille Klenzendorf was born in Oldenburg, Lower Saxony, Germany on October 22, 1971. She grew up in Forest, Baden-Würtemberg, Germany, where she graduated from Schönborngymnasium Bruchsal (German High School) in 1991. Sybille spent a semester in Owatonna, Minnesota, USA, as part of an exchange program between the states of Minnesota and Baden-Würtemberg. Her family moved to the Washington D.C. area in 1991, where Sybille completed her Bachelor of Science degree in biology at George Mason University in 1994 (cum laude).

She then started her Master of Science in Wildlife Sciences at Virginia Polytechnic Institute and State University (VPI&SU) in the fall of 1994. Her thesis, entitled 'Brown bear management in Europe', was a baseline study of brown bear management in 6 European countries to be used for writing a management plan for Austria's recovering brown bear population. The study was funded by the Munich Wildlife Society (WGM), the European Fund for Nature, Program LIFE of the European Union and VPI&SU.

After completing her M.S. degree in May 1997, Sybille volunteered for the Himalayan Wildlife Project in the Karakorum Range of Pakistan to study conservation issues of the Himalayan Brown Bear, an endangered species with only 30-60 animals remaining. She spent 2 months at 15,000 feet of the Deosai Plains in northern Pakistan to locate denning areas of 4 radio-collared bears and to conduct socio-economic evaluations of the surrounding villages to find solutions for local people in conserving bears and trying to make a living at high altitudes.

Returning from Pakistan in August 1997, Sybille started her Ph.D. program in Wildlife Science at VPI&SU to study "Population dynamics of Virginia's hunted black bear population". During the past 4 years, Sybille has participated in data collection for the Cooperative Alleghany Bear Study (CABS) by trapping, handling, and monitoring black bears, and conducting den visitations to evaluate reproduction.

After graduation in May 2002, Sybille plans on moving to the Washington D.C. area to live with her fiancée, William Penhallegon, before their marriage in Filzmoos, Austria, on August 10, 2002.