

**SURVIVAL, FAMILY BREAKUPS, AND DISPERSAL OF YEARLING
AND SUBADULT BLACK BEARS IN WESTERN VIRGINIA**

by

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Thesis submitted to the faculty of the
Virginia Polytechnic Institute & State University
in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

in

Fisheries and Wildlife Sciences

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January 21, 2003

Blacksburg, Virginia

Keywords: black bear, dispersal, family, movements, subadult, survival, Ursus, yearling

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(ABSTRACT)

Reported survival rates, dates of family breakup, and dispersal patterns for yearling and subadult bears in hunted black bear (*Ursus americanus*) populations in North America are scarce. We estimated survival rates of yearling and subadult black bears from a hunted population in western Virginia during 1999 - 2002. We captured and marked 307 different individual yearling and subadult bears on 2 study sites, and attached ear tag transmitters or radio collars to 54 (34M : 20F) 1-year-old, 52 (23M : 29F) 2-year-old, and 35 (8M : 27F) 3-year-old black bears. We used the known fate model in program MARK to estimate annual, non-hunting, and hunting season survival for radio-marked bears of each age and sex class. Additionally, we used mark-recapture data in the recaptures only, dead recoveries, and Burnham's combined models within program MARK to estimate annual survival for each age and sex class. One-, 2-, and 3-year-old female survivorship was 0.87 (95% C.I. 0.78 - 0.92), while 1-year male survivorship was 0.32 (95% C.I. 0.20 - 0.47), and 2- and 3-year-old male survivorship was 0.59 (95% C.I. 0.47 - 0.71) from the Burnham's combined model. Survival rates for 1-year-old females ($\chi^2 = 6.20$, $P = 0.01$) and 2-year-old females ($\chi^2 = 7.74$, $P = 0.01$) were higher than males in each age category, respectively. However, we detected no difference between 3-year-old females and 3-year-old males ($\chi^2 = 2.61$, $P=0.11$), likely due to small sample size of

males ($n = 4$). Low yearling and subadult survival is not likely a cause for alarm due to the importance of adult female survival to population growth and the promiscuous mating system in black bear populations.

Family breakup is an important event in the life history of black bears, marking the initial dispersal and home range construction of yearling bears, and perhaps marking the timing of estrus and breeding opportunities for adult females. We monitored 6 black bear family groups with 12 yearlings (6M : 6F) to determine the timing of family breakup; we intensely monitored 3 of the family groups to document home range establishment and movements by 5 subadult bears (2M : 3F) following separation from their mothers. Estimated dates of family breakup were 28 May and 2 June. Family breakups occurred before peak dates of estrus on our 2 western Virginia study areas. We detected 2 reassociations between a mother and her yearling offspring. Following family breakup, female yearlings ($n = 3$) remained within or partially on their mothers' home range while subadult males ($n = 2$) left their mothers' home ranges. All yearlings ($n = 5$) shared $\geq 50\%$ of post-breakup home range with their mothers.

We studied the movements of 31 (11M : 20F) subadult black bears born on our 2 study areas in western Virginia and 70 (44M : 26F) subadult bears captured during the summer on the study areas for dispersal. No radio-marked, resident, subadult female bears exhibited dispersal behavior while 3 of 11 (27%) radio-marked, resident, subadult males dispersed ($P = 0.04$). Resident and summer capture male bears moved greater distances than females from yearling den location ($\chi^2 = 8.54$, $P = 0.01$, $df = 2$) or summer capture location ($\chi^2 = 22.02$, $P < 0.01$, $df = 2$); no female moved > 10 km between initial and final locations ($x = 2.7$ km, range 0.2 - 9.0 km). The greatest subadult male

movement was 80 km ($x = 13.4$ km, range 0.6 -0.80 km), and dispersal movements primarily occurred within the 1 and 2-year-old age classes. Direction of movement between initial and final locations for dispersing bears was not random (Rayleigh's $r = 0.56$, $P = 0.02$); bears appeared to follow the orientation of the predominant ridgelines and avoided leaving the national forest. Lack of female dispersal may require managers to control local harvest of females providing for continued reproduction and growth within some areas.

ACKNOWLEDGEMENTS

I am greatly indebted to many people and organizations that contributed to the success of this project. First, financial support came from Virginia Polytechnic Institute and State University, the Virginia Department of Game and Inland Fisheries, United States Forest Service, and the United States Geological Service – Biological Resources Division.

The Virginia Bear Hunter's Association (VBHA) deserves a big thanks for their financial contributions, involvement, and support for this research. Special thanks to Ben Wanger and the Briery Branch Group, Tony Hinkle and Jerry Snyder and the Feedstone Hunt Club, Pete McDorman, and Danny Thorn, the current president of the VBHA.

A huge thanks to my advisor Dr. Michael Vaughan for providing me this opportunity to work with bears and learn so much about the wildlife profession. I'd also like to thank my advising committee members: Dr. Dean Stauffer for the statistical advice and help, and Dr. Jim Berkson for the critical comments and presentation critiques. The secretaries in Cheatham deserve great thanks for assisting me in getting through this program and the research. Carol, Linda, Valerie, Holly, Ramona, Peggy, and Arlice have done everything from taking care of financial concerns to answering my most mundane questions. Thanks to all of my fellow graduate students who have made this project a worthwhile experience, especially Shannon Keane who saved me much frustration with her savvy skills at formatting in Word. Special thanks to Andrew Bridges, Rachel Gray, Sybille Klenzendorf, Colleen Olfenbuttel, Deb O'Neill, and Gyasi Quince for all the shared bear data, experience, and adventures.

Virginia Department of Game and Inland Fisheries biologists and biologist assistance contributed greatly to this project through their efforts during trapping and den seasons. Summer trapping would not have been nearly as successful without the help of Oliver Burkholder, Fred Frenzel, Joe Huffer, Bill Mohler, John Pound, Roger Propst, Kenny Sexton, Gene Sours, Roy Schwartz, and Wayne Lee Zollman. Biologists Al Bourgeois, Dave Kocka, and Denny Martin have been of enormous help in the field and in working out the details for trapping and den seasons. Carole Martin, who keeps the show running at the Verona office, was of almost daily assistance. Dave Steffen has always been a friendly face and a huge supporter of this project. Special thanks to Jerry Blank, who worked long hours with the northern crew to shape us into bear trappers. Jerry contributed greatly to the study with his dedication to Virginia's black bears and teaching the graduate students, technicians, and volunteers the safety involved in bear research. Thanks for not chopping off my hair when I arrived on the northern study site and for the delicious (but rather small) deer jerky rewards we received sporadically.

I owe many good friendships, and my sanity, to the great technicians and volunteers who spent endless hours doing fieldwork and living in the "Shack." Thanks to Liz Baillie, Rich Bard, Jodi Fox, Julie King, Karen Murray, Nick Nycum, Mark Robb, Pat Sharkey, Jeff Sikich, John Simmons, Mark Szydlo, and Lindsay Towns. A special thanks to Nicole Rein, whose lack of musical knowledge and slow ATV driving gave me countless hours of amusement, but were far surpassed by her superb organizational skills, commitment to the project, and wonderful company. Somehow we all survived surprise hail storms, high winds, early mornings, late evenings, long days (and sometimes nights),

broken down trucks, atv races, and this Alabama boy driving on icy roads. I'll never forget the experiences we shared and wish the best for all yall.

My experience has been all the better by the support I've received from family and friends while in Virginia. Thanks to Johnster, Jethro, and Jeffrey who have made my forays from Virginia into great times in Alabama and Tennessee. Dad, you have taught me more by example than you may ever realize and I thank you for that. My mom and brother have always been concerned for my well being as I've been away from home and in the woods. I've enjoyed your visits, calls, and all your support. I'd like to give special thanks to my Paw Paw Alexander who appears to have passed along his "chasin' down critters and pickin' up snakes" genes to me.

And all my thanks and love to Stephanie, my wife. Sometimes, we ourselves have been more of a bear to wrestle than those on the project. I look forward to many more years together and to our next adventure.

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CHAPTER 1: INTRODUCTION, JUSTIFICATION, AND OBJECTIVES

INTRODUCTION

Black bears (*Ursus americanus*) have been present in Virginia for centuries (Martin and Steffen 2000). As with other large North American mammals, black bears have been harvested by humans for food, clothing, and material benefit. In Virginia, black bears have become a valued wildlife resource for hunters, photographers, and outdoor enthusiasts. Over the past decade, the black bear harvest in Virginia has increased steadily (Martin and Steffen 2000), concurrent with an apparent growing population (Martin and Steffen 2000, Klenzendorf 2002). Until the initiation of the Cooperative Alleghany Bear Study (CABS), little was known of western Virginia's hunted black bear population since most research had been conducted on unhunted populations in Shenandoah National Park, Great Dismal Swamp National Wildlife Refuge, and Mount Rogers Recreation Area (Carney 1985, Garner 1986, Hellgren 1988, Comley 1993, Kasbohm 1994, Schrage 1994).

In response to the lack of biological and ecological data on the hunted black bear population of western Virginia, CABS was initiated in 1994 as a partnership between the Virginia Department of Game and Inland Fisheries (VDGIF), the United States Forest Service (USFS), and Virginia Polytechnic Institute and State University (VPI&SU). Objectives of CABS include: determine age-specific birth and death rates; determine population growth rates; determine regional density levels; assess importance of factors that influence birth and death rates; estimate the number of black bears in Virginia's hunted bear population; assess indices of population size; develop population models; determine habitat use patterns; assess the quality of Virginia's bear habitat; determine

seasonal distribution patterns; and recommend long-term management strategies for black bears in Virginia (Bridges et al. 2002). This study specifically focused on estimating yearling and subadult (2 and 3 year olds) survival rates, determining the timing of family breakup, and determining dispersal patterns of yearling and subadult black bears. These specific objectives have not been the focus of past CABS studies because of the limited techniques available to achieve the objectives and because of the time and effort required to obtain an adequate sample size.

JUSTIFICATION

Survival and dispersal of yearling and subadult bears are a vital, yet often overlooked, components of black bear population dynamics. Wildlife scientists studying bears have conducted few studies on yearling and subadult black bears in North America (Rogers 1987, Bunnell and Tait 1985, Schwartz and Franzmann 1992). Many researchers conducting black bear studies are reluctant to collar fast growing subadult animals because of the potential for collar related injuries (Higgins 1997), and dispersing individuals are difficult to monitor and recapture. Additionally, most black bear studies focus on adult females for reproductive and survival demographics (Eberhardt 1990). Studying family breakup and the dissolution of the bond between adult female bears and their offspring requires monitoring the entire family group. Thus, rarely are dates of family breakups estimated for black bear populations, or survival estimates and dispersal patterns attained for yearling and subadult bears.

Determining when young bears separate from their female parent (i.e. duration of parental care) may help researchers better understand family dissolution and the onset of

estrus in adult females. In addition, family breakup may mark the beginning of home range establishment and dispersal behavior for yearling and subadult bears.

Knowledge of yearling and subadult survival and dispersal is important to managers and researchers of black bears populations for a number of reasons (Alt 1978). Age-specific survival and dispersal rates are often necessary for black bear population models, which can aid in achieving management goals (Klenzendorf 2002). Survival of subadult bears represents recruitment into the reproductively active adult population. Dispersal is important for its role in establishing and maintaining black bear populations. Subadult bears are capable of traveling long distances (Rogers 1987), which may have implications for increasing genetic variability among bear populations, the usefulness of bear refuges, and survival risks (Clevenger and Pelton 1990). Immigration and emigration of subadult male bears may be responsible for maintaining bear populations in heavily hunted sites, as reported in Idaho (Beecham 1980). Dispersal has consequences for bears by bringing them into closer contact with human induced forms of mortality, including harvest and automobile collisions (Schwartz and Franzmann 1992).

Determining dispersal patterns of subadult bears may aid our understanding of how bears pioneer new areas and locate vacant habitat. Dispersal is critical to reducing the genetic isolation between island populations and introducing genetic variability in isolated bear populations in Virginia and throughout the southeastern United States (Hellgren and Vaughan 1994).

OBJECTIVES

Survival - Specific objectives of this study were to determine survival rates for male and female yearling and subadult black bears, compare survival rate estimation from radio-collared data and mark-recapture data analysis, and compare subadult survival rates with other North American bear populations.

Family - Specific objectives of this study were to determine the mean date of family breakup in western Virginia, determine if reassociations occur between family members following family breakup, determine if the timing of family breakup coincides with onset of estrus, and determine differences between male and female offspring in post-breakup home range use.

Dispersal - Specific objectives of this study were to determine behavioral differences in dispersal between male and female subadult black bears, determine if distance movements varied between sexes, determine the time of year dispersal occurs, determine if bears dispersed randomly, and examine the relationship between dispersal distance and survival.

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CHAPTER 2: YEARLING AND SUBADULT BLACK BEAR SURVIVAL IN A HUNTED WESTERN VIRGINIA POPULATION

ABSTRACT

Reported survival rates for yearling and subadult bears in hunted black bear populations in North America are scarce. We estimated survival rates of yearling and subadult black bears from a hunted population in western Virginia during 1999 - 2002. We captured and marked 307 different individual yearling and subadult bears on 2 study sites, and attached ear tag transmitters or radio collars to 54 (34M : 20F) 1-year-old, 52 (23M : 29F) 2-year-old, and 35 (8M : 27F) 3-year-old black bears. We used the known fate model in program MARK to estimate annual, non-hunting, and hunting season survival for radio-marked bears of each age and sex class. Additionally, we used mark-recapture data in the recaptures only, dead recoveries, and Burnham's combined models within program MARK to estimate annual survival for each age and sex class. One-, 2-, and 3-year-old female survivorship was 0.87 (95% C.I. 0.78 - 0.92), while 1-year male survivorship was 0.32 (95% C.I. 0.20 - 0.47), and 2- and 3-year-old male survivorship was 0.59 (95% C.I. 0.47 - 0.71) from the Burnham's combined model. Survival rates for 1-year-old females ($\chi^2 = 6.20$, $P = 0.01$) and 2-year-old females ($\chi^2 = 7.74$, $P = 0.01$) were higher than males in each age category, respectively. However, we detected no difference between 3-year-old females and 3-year-old males ($\chi^2 = 2.61$, $P = 0.11$), likely due to small sample size of males ($n = 4$). Low yearling and subadult survival is not likely a cause for alarm due to the importance of adult female survival to population growth and the promiscuous mating system in black bear populations.

INTRODUCTION

Few studies have been conducted on the survival of yearling and subadult black bears (*Ursus americanus*) in North America (Bunnell and Tait 1985, Schwartz and Franzmann 1992). Many researchers conducting black bear studies are reluctant to collar fast growing subadult animals because of the potential for collars to cause injury (Higgins 1997), plus dispersing individuals are difficult to monitor and recapture. Additionally, most black bear studies focus on adult females for reproductive and survival demographics (Eberhardt 1990).

Nonetheless, knowledge of yearling and subadult survival is important to managers and researchers of black bear populations. Age-specific survival rates are necessary components of population models, and can aid managers in achieving population level goals (Klenzendorf 2002). Survival of subadult bears represents recruitment into the reproductively active adult population.

Survival rates for subadult black bears tend to be lower than for adult black bears in North American populations (Bunnell and Tait 1981, Schwartz and Franzmann 1991, Beringer et al. 1998). Subadult bears, especially males, are capable of traveling long distances and have larger home ranges, making them more susceptible to harvest, automobile collisions, and other anthropogenic sources of mortality (Schwartz and Franzmann 1992).

We estimated annual, hunting season, and non-hunting season survival rates from radio-transmitted yearling and subadult bears using the Pollock et al. (1989) modification of the Kaplan-Meier survival estimator (Kaplan and Meier 1958) in program MARK (White and Burnham 1999). We also estimated annual survival rates for

yearling and subadult bears from 4 years of summer capture-recapture data and 3 years of harvest recoveries. The specific objectives of this study were to determine survival rates for male and female yearling and subadult black bears, compare survival rate estimates from radio-collared data and mark-recapture data analysis, and compare subadult survival rates with other North American bear populations.

STUDY AREAS

The Cooperative Alleghany Bear Study (CABS) has 2 study areas in western Virginia separated by approximately 140 km (Figure 1). The 860-km² northern study site is in the George Washington-Jefferson National Forests and is centered in Augusta and Rockingham Counties. The site contains portions of the Dry River and Deerfield Ranger Districts in the Ridge and Valley Province of the Appalachian Mountains. Elevations range between 488m along the base of Little North Mountain and 1,360m at the top of Elliott Knob (Kozak 1970).

The 1,540-km² southern study site is in the George Washington-Jefferson National Forests and encompasses much of Montgomery, Giles, and Craig counties. The study site is in the Blacksburg and Newcastle Ranger Districts in the Ridge and Valley Province of the Southern Appalachian Mountains (United States Department of Agriculture, 1965). Elevation ranges from 492m along the Craig Creek drainage to 1,378m at Mountain Lake.

At Dale Enterprise in the adjacent Shenandoah Valley, the average temperatures vary between 0.3 °C and 22.9 °C over the year, with an average of 11.8 °C. Average yearly precipitation is 86 cm and occurs mostly between April and September. Average

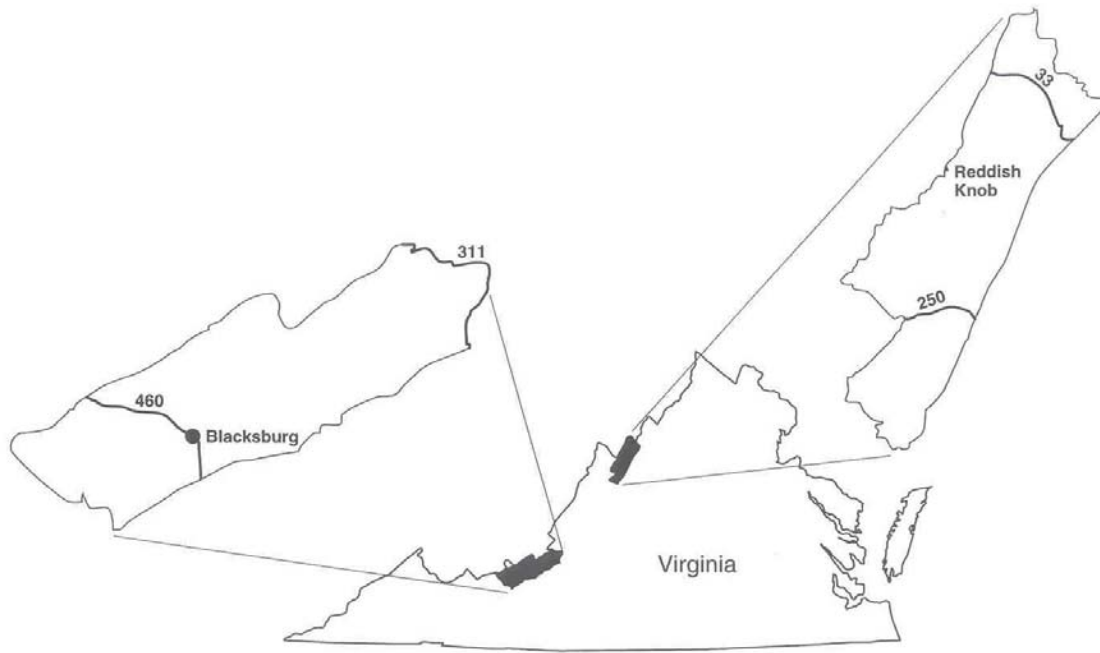


Figure 1. The northern and southern study sites of the Cooperative Alleghany Bear Study in the George Washington - Jefferson National Forests, Virginia.

snowfall is 71 cm/year. The mountains of the study area usually receive more precipitation and average 2.8-5.6 °C cooler than in the Shenandoah Valley (Rawinski et al 1994).

Vegetation in the study sites is similar. Forest cover types on the study areas include: eastern hemlock (*Tsuga canadensis*), sugar maple-beech-yellow birch (*Acer saccharum*, *Fagus grandifolia*, *Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak-black oak-northern red oak (*Q. alba*, *Q. velutina*, *Q. rubra*), northern red oak, yellow poplar-white oak-northern red oak (*Liriodendron tulipifera*), eastern white pine (*P. strobus*), and barren and brush cover such as mountain laurel (*Kalmia latifolia*) or scrub oak (*Q. ilicifolia*) (Rawinski et al. 1994).

METHODS

Fieldwork was conducted during June 1999 - August 2002. We trapped bears during June - August each year (1999-2002) with spring-activated Aldrich foot snares and culvert traps, and we entered the dens of radio-collared bears during January – March each year. We used a 2:1 mixture of ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (Rompun, Bayer Corporation, Shawnee Mission, KS; concentration of 300 mg/ml) at a dosage rate of 1cc/45.4 kg (100 lbs.) of body weight to immobilize bears. Drug was administered with a Capchur gun (Palmer Chemical Company, Douglasville, GA) or jab stick. We took standard body measurements and drew blood samples. We extracted the first premolar for age estimation by cementum annuli analysis (Willey 1974) at Matson's Laboratory LLC (Milltown, MT). We attached ear tag transmitters to a sample of subadult bears

during the handling process. After all handling was complete, Antagonil (yohimbine hydrochloride, Wildlife Laboratories, Incorporated, Fort Collins, CO; concentration of 5 mg/ml) was administered at a dosage of 2cc/45.4 kg as an antagonist to the xylazine hydrochloride.

We located transmitter-equipped bears with ground telemetry to determine location and monitor survival. We supplemented ground telemetry with aerial telemetry approximately every 28 days, and we gave priority to bears not found during the ground surveys. Ground telemetry using Telonics (Telonics, INC., Mesa, AZ) receivers and H-antennas was conducted along an extensive station system established along forest roads and trails. We walked in on ear tag transmitters emitting mortality signals to determine cause of death or to retrieve dropped transmitters. We attempted to monitor all yearling and subadult bears at least 1/week during the study.

We designated bears 1-year-old as yearlings, 2- and 3-year-olds as subadults, and ≥ 4 years old as adults for survival analysis. We attached ear tag transmitters or radio-collars to a sample of yearling and subadult bears captured in the den and during summer trapping. We removed from our analysis bears that died due to researcher-induced mortality, and censored radio-collared bears from known fate analysis if not detected for > 30 days. We confirmed the mortality of harvested bears with Virginia Department of Game and Inland Fisheries (VDGIF) game check cards, voluntary return of ear tags and/or radio transmitters by hunters, and calls to nearby states (i.e. West Virginia) on harvest of CABS marked bears.

We used the program MARK (White and Burnham 1999) version of Kaplan-Meier's (1958) product-limit estimator modified by Pollock et al. (1989) to estimate

survival for radio-collared individuals. The known fate procedure allowed for the staggered entry of radio-collared bears throughout the study. Within the known fate analysis, we estimated annual survival, non-hunting season survival (January - September) and hunting season survival (October - December). We further subdivided hunting season by method of hunt (archery, rifle only, hunting with hounds) to estimate survival for all age and sex classes. The assumptions of the known fate estimator include 1) animals of a particular sex and age class were randomly sampled, 2) survival times were independent for individuals, 3) capture of an animal or placement of radio transmitter on the animal had no influence on its survival, 4) the censoring mechanism is random (i.e. mechanism is not related to the fate of the individual), and 5) newly tagged animals and previously tagged animals had the same survival probability (Pollock et al. 1989).

We estimated age- and sex-specific annual survival rates from mark-recapture data using 3 models within program MARK. We developed a set of models *a priori* that related survivorship to age and sex class, without annual variation, based on earlier analyses of subadult and adult survivorship during this study (Klenzendorf 2002). We used 4 summers of capture data (1999 - 2002) in a standard CJS model (Cormack 1964, Jolly 1965, Seber 1965), 3 years of harvest returns (1999 - 2001) in a dead returns model (Seber 1970, Anderson et al. 1985, Catchpole et al. 1995), and the combined data in Burnham's combined model (Burnham 1993) for survival estimates.

We ran a model in each of 3 mark-recapture models that separately estimated survival for each age and sex class. We compared survival estimates for each age class within sex classes with chi-square analysis in program CONTRAST (Hines and Sauer

1989). Tests were considered significant at $\alpha = 0.05$. Results were used to support the inclusion of further models that combined the survival probabilities of different age classes of males and females into pooled survival estimates (e.g. pooling 2- and 3-year-old males).

We fitted a general model, $\Phi_{(as)}$, $p_{(as)}$, consisting of separate survival and recapture parameters for all age and sex classes to test model goodness-of-fit (GOF) as recommended by Lebreton et al. (1992) and Cooch and White (1999). The symbol *as* represents separate age and sex classes of bears (Lebreton et al. 1992). This model represented the most parameterized model and was assessed using a bootstrap GOF test. We expected our data to be somewhat over-dispersed (i.e. lack of fit for an open mark-recapture analysis) due to the influence of behavioral and dispersal differences among ages and sexes. If warranted by the bootstrap GOF test, \hat{c} , the variation inflation factor, is calculated, which can be used to adjust subsequent estimates in the CJS model (Burnham and Anderson 1998). We took a conservative approach and used the \hat{c} if the bootstrap GOF test was significant at $P < 0.20$ (Cooch and White 1999). We calculated \hat{c} by 2 methods; 1) dividing the deviance of the general model by the average deviance of the bootstrap simulations, and 2) dividing the observed \hat{c} from the general model by the average \hat{c} from the bootstrap simulations (Cooch and White 1999). Since it is not clear which method is more valid, we conservatively used the larger estimate (Cooch and White 1999).

We estimated Φ , a survival rate confounded with emigration, from mark-recapture data in the CJS model (recaptures only model; Cooch and White 1999). All trapped animals were marked with ear tags and a lip tattoo and released for possible

recapture in succeeding summers. We estimated survival for each age and sex class and for pooled combinations of ages (i.e. combining survival parameter for all ages of females and all ages of males, pooling of 2- and 3-year-old males, and pooling of 2- and 3-year-old females). We kept recapture probability, p , constant across all age and sex classes or varied by sex in all models.

We estimated survivorship, S , from the recovery of harvested bears in the dead recoveries model. Bears survived the interval with a probability of S , and dead bears (i.e. harvested) had a recovery probability of r between trapping events (Cooch and White 1999). We estimated survival for each age and sex class and for some pooled age classes within sex. We kept recovery probability constant across all age and sex classes.

We also derived survival estimates from Burnham's combined model, a combination of the previous 2 models. It directly estimates survival, S , instead of Φ as in the CJS model. We estimated survival for each age and sex class and for varying combinations of age classes. In most models we kept recapture probability, p , recovery rate, r , and site fidelity, F , constant for all age and sex groups.

Assumptions of the CJS model include 1) all marked animals have the same probability of recapture, 2) all marked animals have the same probability of survival, 3) marks are not lost or missed, and 4) marking intervals are brief (Seber 1986, Cooch and White 1999). The dead recovery analysis assumes constant reporting rates of harvested animals and correct identification of harvested individuals (Cooch and White 1999).

We used adjusted Akaike's Information Criterion (AICc; Akaike 1985, Hurvich and Tsai 1989) to select the most parsimonious model (i.e. lowest AICc value) within each of the 3 mark-recapture models in reporting survival estimates for each sex and age

class (Burnham and Anderson 1992, 1998, Cooch and White 1999). AICc is a numerical estimation of the balance between the number of parameters needed to explain the data and fit (lower deviance) of the model. Low AICc models with delta AICc varying by < 2 were considered equivalent, and we chose the model with the fewest parameters as the one best explaining the data (Burnham and Anderson 1998). When using \hat{c} , we used quasi-likelihood modified criteria (QAICc) instead of AICc (Cooch and White 1999).

We report 95% confidence intervals for all survival estimates. We compared known fate survival estimates between 1-year-old males and 1-year-old females, 2-year-old males and 2-year-old females, 3-year-old males and 3-year-old females, and between 2-year-old males and 3-year-old males using chi-square analysis in program CONTRAST (Hines and Sauer 1989). We also compared survival estimates between 1-year-old males and a pooled sample of 2- and 3-year-old male estimate from the most parsimonious Burnham's combined model. All tests were considered significant at $\alpha = 0.05$.

RESULTS

CABS personnel captured 307 different yearling and subadult bears on the 2 study areas between June 1999 and August 2001. We captured 111 (78M : 33F), 107 (67M : 40F), and 134 (95M : 39F) yearling and subadult black bears during the 1999, 2000, and 2001, respectively. We recorded the mortalities of 4 1-year-old, 7 2-year-old, and 2 3-year-old females, and 41 1-year-old, 38 2-year-old, and 11 3-year-old males that were harvested the same year as captured by CABS personnel during 1999-2001. An additional 12 (11M : 1F) black bears were harvested as a subadult, but not during the same year as capture. CABS documented 3 non-harvest related mortalities of marked

yearling and subadult males. One yearling female died after we captured her and her family at their den site. She was removed from further study. Automobiles killed 2 subadult males, 1 2-year-old and 1 3-year old; neither was wearing a radio-transmitter.

We attached ear tag transmitters or radio collars to 54 (34M : 20F) 1-year-old, 52 (23M : 29F) 2-year-old, and 35 (8M : 27F) 3-year-old black bears. We observed mortalities of 1 1-year-old, 2 2-year-old, and 1 3-year-old females, and 10 1-year-old, 8 2-year-old, and 2 3-year-old males who were wearing radio-transmitters at time of death. Harvest was the only cause of mortality (100%) for all yearling and subadult bears wearing radio-transmitters. Harvest (98%) and automobile collisions (2%) were known sources of mortality for marked (i.e. ear tagged and lip tattoos) yearling and subadult black bears.

Estimated survival from the known fate model was 1.00 during the non-hunting season (January – September) for all sex and age classes. Annual survival rates for yearling, 2-year-old, and 3-year-old females were 0.90 (0.52 – 0.99), 0.86 (0.59 – 0.97), and 0.94 (0.66 – 0.99), respectively. Estimated survival of pooled 2- and 3-year-old females was 0.90 (0.74 – 0.97) (Table 1). Yearling, 2-year-old, and 3-year-old male annual survival rates were 0.53 (0.32 – 0.72), 0.42 (0.20 – 0.67), and 0.54 (0.15 – 0.88), respectively. Estimated survival of pooled 2- and 3-year-old males was 0.45 (0.25 – 0.67) (Table 2). Further breakdown of survival rates by hunting season method for females and males are presented in Tables 1 and 2, respectively.

Chi-square test results revealed that survival estimates did not differ between 1-, 2-, or 3-year-old females for all 3 mark-recapture models (Table 3). Neither did we detect a difference between survival estimates of 2- and 3-year males for all 3 models.

Table 1. Kaplan-Meier estimates (Pollock et al. 1998) of annual and interval survival rates (95% C.I.) for yearling and subadult female black bears radio-collared between 1999-2002 for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia.

	Age Class			
	Yearling Females (n = 1 - 8)	2-year-old Females (n = 1 - 13)	3-year-old Females (n = 1 - 8)	2-and 3-year-old Females (n = 1 - 21)
Interval				
Annual	0.90 (0.52 - 0.99)	0.86 (0.59 - 0.97)	0.94 (0.66 - 0.99)	0.90 (0.74 - 0.97)
Non-hunting season	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)
Pooled hunting seasons	0.89 (0.51 - 0.99)	0.89 (0.66 - 0.97)	0.95 (0.73 - 0.99)	0.93 (0.79 - 0.98)
Archery season ^a	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)
Rifle season ^b	0.90 (0.53 - 0.99)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)
Hound season ^c	1.00 (1.00 - 1.00)	0.88 (0.61 - 0.97)	0.95 (0.73 - 0.99)	0.92 (0.78 - 0.97)

^a Second Saturday of October through second Saturday of November (approximately 4 weeks).

^b Fourth Monday of November through first Friday of January (approximately 6 weeks) with opening date to last Saturday of November as rifle use only (e.g. Hunters not allowed to use hounds to pursue bears; approximately 1 week).

^c First Monday of December through first Friday of January (approximately 5 weeks). Hunters allowed to use hounds to pursue bears.

Table 2. Kaplan-Meier estimates (Pollock et al. 1998) of annual and interval survival rates (95% C.I.) for yearling and subadult male black bears radio-transmitted between 1999-2002 for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia.

	Age Class			
	Yearling Males (n = 1 - 17)	2-year-old Males (n = 1 - 13)	3-year-old Males (n = 1 - 4)	2-and 3-year-old Males (n = 1 - 17)
Interval				
Annual	0.53 (0.32 - 0.72)	0.42 (0.20 - 0.67)	0.54 (0.15 - 0.88)	0.45 (0.25 - 0.67)
Non-hunting season	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)	1.00 (1.00 - 1.00)
Pooled hunting season	0.53 (0.33 - 0.72)	0.52 (0.29 - 0.74)	0.54 (0.16 - 0.88)	0.52 (0.32 - 0.72)
Archery season ^a	0.91 (0.71 - 0.98)	0.94 (0.67 - 0.99)	0.80 (0.31 - 0.97)	0.89 (0.66 - 0.97)
Rifle season ^b	0.87 (0.60 - 0.97)	1.00 (1.00 - 1.00)	0.75 (0.25 - 0.97)	0.94 (0.67 - 0.99)
Hound season ^c	0.60 (0.35 - 0.81)	0.46 (0.22 - 0.72)	1.00 (1.00 - 1.00)	0.53 (0.29 - 0.76)

^a Second Saturday of October through second Saturday of November (approximately 4 weeks).

^b Fourth Monday of November through first Friday of January (approximately 6 weeks) with opening date to last Saturday of November as rifle use only (e.g. Hunters not allowed to use hounds to pursue bears; approximately 1 week).

^c First Monday of December through first Friday of January (approximately 5 weeks). Hunters allowed to use hounds to pursue bears.

Table 3: Chi-square test results for comparisons of survival estimates from mark-recapture data^a between all age classes for female and male black bears captured by the Cooperative Alleghany Bear Study between 1999-2002 in the George Washington-Jefferson National Forest, Virginia.

Comparison of Age classes	CJS		Model Dead Recoveries		Burnham's combined	
	χ^2	P	χ^2	P	χ^2	P
1- and 2-year-old females	0.02	0.88	0.13	0.72	0.15	0.70
1- and 3-year-old females	1.00	0.32	1.42	0.23	1.51	0.22
2- and 3-year-old females	0.95	0.33	0.01	0.92	1.43	0.23
1- and 2-year-old males	3.19	0.07	2.71	0.10	4.93	0.03
1- and 3-year-old males	3.49	0.06	6.42	0.01	13.39	0.01
2- and 3-year-old males	0.24	0.62	1.21	0.27	2.80	0.09

^a See Appendix 1 for survival estimates and 95% C.I. for individual age and sex classes used in Ch-square tests.

One-year-old males had lower survival ($\chi^2 = 4.93$, $P = 0.03$) than 2-year-old males in Burnham's combined model and 1-year-old males had lower survival than 3-year-old males in the dead recoveries ($\chi^2 = 6.42$, $P = 0.01$) and Burnham's combined ($\chi^2 = 13.49$, $P = 0.01$) models. We did not detect a difference between these same age classes in the CJS model or for a comparison of 1-year-old and 2-year-old males in the dead recovery model, but in each case, the results approached significance (Table 3).

From our bootstrap GOF analysis, we found that our data set was over-dispersed ($P=0.09$). We calculated \hat{c} as 1.32, indicating slightly over-dispersed data for the CJS analysis (Anderson et al. 1994). Recapture rates for 1-, 2-, and 3-year-old females and males were 0.57, 0.69, 0.54, 0.77, 0.43, and 0.52, respectively; however models with the lowest QAICc values were simpler models and had a constant recapture probability for all sex and age classes. Four CJS models differed by < 2 in delta QAICc, however 1 model needed 1 fewer parameters to explain the data (Table 4). The most parsimonious model for the CJS model was $\text{Phi}_{(\text{as } 1+2+3\text{F}, 1\text{M}, 2+3\text{M})}$, $\text{p}_{(.)}$ where survival probability was the same for 1-, 2-, and 3-year-old females (0.76 (0.55 – 0.89)), separate for yearling males (0.24 (0.12 – 0.42)), and the same for 2- and 3-year-old males (0.47 (0.33 – 0.62)) (Table 5).

Models we evaluated for survival estimates from the dead recoveries analysis differed little in delta AIC (Table 6). As in the CJS analysis, the most parsimonious model modeled the survival probability in the same way, $\text{S}_{(\text{as } 1+2+3\text{F}, 1\text{M}, 2+3\text{M})}$. Survival rates were 0.82 (0.69 – 0.90) for 1-, 2-, and 3-year old females, 0.16 (0.06 – 0.35) for yearling males, and 0.39 (0.22 – 0.60) for 2- and 3-year-old males. Dead recovery analysis computed slightly higher survival rates for females and slightly lower survival

Table 4. QAICc scores and number of parameters for a selection of CJS survival models for yearling and subadult female and male black bears captured between 1999-2002 for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia.

Model ^a	QAICc	Delta QAICc	QAICc Weight	Number of Parameters
{Phi _(as 1+2+3F, 1M, 2+3M) , p _(.) }	395.72	0.00	0.31	6
{Phi _(as 1+2F, 3F, 1M, 2+3M) , p _(.) }	396.52	0.80	0.21	7
{Phi _(as 1F, 2+3F, 1M 2+3M) , p _(.) }	397.35	1.63	0.14	7
{Phi _(as 1+2+3F, 1M, 2M, 3M) , p _(.) }	397.50	1.79	0.13	7
{Phi _(as 1+2+3F, 1+2+3M) , p _(.) }	398.72	3.00	0.07	5
{Phi _(as 1F, 2+3F, 1M, 2+3M) , p _(s) }	398.84	3.12	0.07	8
{Phi _(as 1+2+3F, 1+2+3M) , p _(s) }	399.92	4.20	0.04	6
{Phi _(as 1F, 2F, 3F, 1M, 2M, 3M) , p _(.) }	400.40	4.69	0.03	9
{Phi _(as 1F, 2F, 3F, 1M, 2M, 3M) , p _(s) }	402.08	6.36	0.01	10
{Phi _(as) , p _(as) }	412.35	16.64	0.00	16

^a Model notation follows Lebreton et al (1992), Phi represents survival and p represents recapture probability. Subscripts, as, s, and ., represent parameter modeled varied by age and sex class, varied by sex, and was held constant, respectively. Within subscript as, 1F, 2F, 3F, 1M, 2M, and 3M represent 1-year-old females, 2-year-old females, 3-year-old females, 1-year-old males, 2-year-old males, and 3-year-old males, respectively. A + between age subscripts indicate survival parameter was the same for those ages. The lone as parameter indicates that the parameter was allowed to vary independently with respect to age and sex to give the most parameterized model.

Table 5: Comparison of 3 estimates of annual survival rates for yearling and subadult black bears captured during 1999-2002 (excluding handling mortalities) for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia. All estimates are taken from most parsimonious model for each survival analysis.

Age class	Cormack – Jolly - Seber		Dead recoveries		Burnham's combined model	
	Estimate	95% C.I.	Estimate	95% C.I.	Estimate	95% C.I.
Female ^a						
1, 2, and 3 yr pooled	0.76	0.55 – 0.89	0.82	0.69 – 0.90	0.87	0.78 – 0.92
Male ^b						
1yr	0.24	0.12 – 0.42	0.16	0.06 – 0.35	0.32	0.20 – 0.47
2 and 3 yr pooled	0.47	0.33 – 0.62	0.39	0.22 – 0.60	0.59	0.47 – 0.71

^a For all models, the most parsimonious model grouped 1-, 2-, and 3-year-old females having the same survival rate. Sample sizes for 1-, 2-, and 3-year-old females were n = 26, 40, and 25, respectively.

^b For all models, the most parsimonious model grouped 2- and 3-year-old males having the same survival rate. Sample sizes for 1-, 2- and 3-year-old males were 83, 103, and 30, respectively.

Table 6. Dead recoveries (Seber 1970, Anderson et al. 1985, Catchpole et al. 1995) survival models ordered by their AICc weights for yearling and subadult female and male black bears captured between 1999-2001 for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia.

Model ^a	AICc	Delta AICc	AICc Weight	Number of Parameters
{S _(as 1+2+3F, 1M, 2+3M) , r _(.) }	448.31	0.00	0.22	6
{S _(as 1+2+3F, 1M, 2M, 3M) , r _(.) }	448.31	0.00	0.22	7
{S _(as 1+2F, 3F, 1M, 2M, 3M) , r _(.) }	448.77	0.46	0.18	8
{S _(as 1F, 2+3F, 1M, 2+3M) , r _(.) }	449.80	1.49	0.11	7
{S _(as 1+2+3F, 1M, 2M, 3M) , r _(s) }	450.42	2.11	0.08	8
{S _(as 1+2F, 3F, 1M, 2M, 3M) , r _(s) }	450.71	2.40	0.07	9
{S _(as 1F, 2F, 3F, 1M, 2M, 3M) , r _(.) }	450.75	2.45	0.07	9
{S _(as 1+2+3F, 1+2+3M) , r _(.) }	451.13	2.82	0.05	5

^a Model notation follows Lebreton et al (1992), S represents survival and r represents recovery probability. Subscripts, as, s, and ., represent parameter modeled varied by age and sex class, varied by sex, and was held constant, respectively. Within subscript as, 1F, 2F, 3F, 1M, 2M, and 3M represent 1-year-old females, 2-year-old females, 3-year-old females, 1-year-old males, 2-year-old males, and 3-year-old males, respectively. A + between age subscripts indicate survival parameter was the same for those ages.

rates for males than the CJS model, although confidence intervals overlapped for all age and sex classes (Table 5). In Burnham's combined model, delta AICc differed < 2 in 4 models (Table 7). As in the CJS and dead recoveries models, survivorship was best modeled with a combined survival probability for 1-, 2-, and 3-year-old females, separate survival probability for 1 year-old males, and a combined survival probability for 2- and 3-year-old males. Most parsimonious model was $S_{(as\ 1+2+3F, 1M, 2+3M)}, p_{(.)}, r_{(.)}, F_{(.)}$. Survival rates were 0.87 (0.78 – 0.92) for females, 0.32 (0.20 – 0.47) for 1-year-old males, and 0.59 (0.47 – 0.71) for 2- and 3-year-old males (Table 5).

Known fate survival rates were higher for 1-year-old females ($\chi^2 = 6.20, P = 0.01$) and 2-year-old females ($\chi^2 = 7.74, P = 0.01$) than for males in each age category, respectively. However, we detected no difference between 3-year-old males and 3-year-old females ($\chi^2 = 2.61, P = 0.11$), or between 2-year-old males and 3-year-old males ($\chi^2 = 0.19, P = 0.66$). Survival rate estimates from Burnham's combined analysis were higher for pooled 2- and 3-year-old males than for 1-year-old males ($\chi^2 = 14.02, P < 0.01$).

DISCUSSION

As reported in other North American populations (Bunnell and Tait 1985, Elowe and Dodge 1989, Schwartz and Franzmann 1992, Beringer et al. 1998), harvest represented the majority of bear mortality; yearling and subadult males were disproportionately represented in the harvest. The known fate survival analysis produced higher survival rates for 1-, 2-, and 3-year-old females than all 3 mark-recapture models; the Burnham combined model estimate was most similar to the known fate estimates. The known fate analysis also produced higher survival rates for yearling males, but not

Table 7. Burnham combined (Burnham 1993) survival models ordered by their AICc weights for yearling and subadult female and male black bears captured between 1999-2002 for the Cooperative Alleghany Bear Study, George Washington-Jefferson National Forests, Virginia.

Model	AICc	Delta AICc	AICc Weight	Number of Parameters
$\{S_{(as\ 1+2+3F, 1M, 2M, 3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	901.45	0.00	0.28	9
$\{S_{(as\ 1+2F, 3F, 1M, 2M, 3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	901.75	0.30	0.24	10
$\{S_{(as\ 1F, 2+3F, 1M, 2M, 3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	902.70	1.25	0.15	10
$\{S_{(as\ 1+2+3F, 1M, 2+3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	903.04	1.60	0.12	8
$\{S_{(as\ 1F, 2F, 3F, 1M, 2M, 3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	903.64	2.19	0.09	11
$\{S_{(as\ 1F, 2F, 3F, 1M, 2M, 3M)}, p_{(s)}, r_{(.)}, F_{(.)}\}$	904.73	3.28	0.05	12
$\{S_{(as\ 1F, 2F, 3F, 1M, 2M, 3M)}, p_{(.)}, r_{(.)}, F_{(s)}\}$	904.83	3.38	0.05	12
$\{S_{(as\ 1F, 2F, 3F, 1M, 2M, 3M)}, p_{(s)}, r_{(.)}, F_{(s)}\}$	906.67	5.23	0.02	13
$\{S_{(as\ 1+2+3F, 1+2+3M)}, p_{(.)}, r_{(.)}, F_{(.)}\}$	912.40	10.95	0.00	7

^a Model notation follows Lebreton et al (1992), S, p, r, and F represents survival, recapture probability, recovery probability, and site fidelity, respectively. Subscripts, as, s, and ., represent parameter modeled varied by age and sex class, varied by sex, and was held constant, respectively. Within subscript as, 1F, 2F, 3F, 1M, 2M, and 3M represent 1-year-old females, 2-year-old females, 3-year-old females, 1-year-old males, 2-year-old males, and 3-year-old males, respectively. A + between age subscripts indicate parameter was constant for those ages.

for 2- and 3-year-old male bears, with the exception of Burnham's combined model. The most parsimonious models for all 3 mark-recapture models grouped survival probability and calculated 1 estimate for 1-, 2-, and 3-year-old females and for 2- and 3-year-old males. We feel confident that the pooling of these survival rates are acceptable since the 3 mark-recapture models used different data sets (i.e. recaptures only, harvest recoveries, and the combined data set) and independently concluded that the age pooling provided the most parsimonious model. Likewise, chi-square analysis failed to show a significant difference between survival estimates between 1-, 2-, and 3-year-old females and between 2- and 3-year-old males for all 3 mark-recapture models (Table 3).

Additionally, the chi-square analysis did not detect a difference between known fate survival estimates of 2-year-old males and 3-year-old males ($P = 0.66$), which strengthens the conclusion that the mark-recapture analyses accurately modeled survival rates as the same for these 2 age classes. Lack of a difference between the survival rates of 3-year-old males and 3-year-old females in the known fate analysis ($P = 0.11$) may be due to small sample size of 3-year-old males ($n = 4$), although the p-value approached significance.

Validity and reliability of survival estimates by statistical analysis is dependent on meeting assumptions, since violations can lead to biased results and false conclusions. We felt comfortable that we met assumptions for the Kaplan-Meier analysis. Assumption 2 (i.e. survival times are independent for individuals) was met since 1-year-old black bears are independent of their mothers by the time hound-training season and hunting season begins in September. We probably met assumption 3 (i.e. transmitter does not influence survival). Klenzendorf (2002) reported that hunter's selectively avoided

harvesting radio-collared females during the first 3 years (1994 - 1996) of the CABS study, when hunters knew that primarily adult females were radio-collared. A bias was not detected for subsequent years on the study (1997 – 1999), or for any other age or sex class (Klenzendorf 2002). Ear tag transmitters may also lessen this bias since they are smaller, possibly less noticeable, and are used on all age and sex classes. We met assumption 5 (i.e. new and old radio-marked bears have the same survival probably) since annual variation in survival was not apparent in this study or previous CABS survival analyses (Klenzendorf 2002).

Assumptions for the CJS model using mark-recapture data are more difficult to meet. Bunnell and Tait (1981) warned that dispersal of the subadult age class is an "unacceptable violation of mark and recapture assumptions." However, survival estimation is more robust to potential failures to meet assumptions than estimates of population size when conducting a CJS analysis (Lebreton et al. 1992). Dispersal from study areas and differences in recapture rates due to behavior is a violation of CJS assumption 1. We addressed the heterogeneity of recapture rates by dividing our sample into age and sex classes for age- and sex-specific survival estimation. Movement off the study areas by subadult dispersal affected only the CJS survival estimates, since harvest recoveries were included in the dead recoveries and Burnham's combined models. Failure to meet assumption 1 would likely underestimate survival of subadult males, particularly 2-year-olds, since dispersal is greater for this age class (CABS, unpublished data) and recapture rate was lowest for this age class.

We also met assumption 2 (i.e. all marked animals have the same survival probability) by separating bears into age and sex classes for analysis. Assumption 3

likely was met since we mark all bears with ear tags and lip tattoos, and some bears with radio transmitters, thus the chance that marked bears kept at least 1 mark was high. We met the assumption of constant reporting rate of dead animals across time and correct identification of harvested individuals for the dead recoveries model since mandatory check-in of harvested bears is regulation in Virginia and did not change during this study. The likelihood of a hunter or check station operator detecting and correctly identifying a marked bear was unestimatable, but believed to be high.

It is difficult to conclude which of the 4 models was best suited for estimating survivorship. The CJS model provides robust survival estimates, but since permanent emigration and mortality are confounded with the survival estimate, the survival estimate was generally believed to be lower than the true survival rate (Cooch and White 1999). The CJS model was likely less accurate than the dead recoveries and combined models since available harvest information was not included. Also, the marking and recapture methods were the same and may have encouraged trap shyness or happiness among individuals. The dead recoveries model uses different methods for marking and recapture (i.e. harvest) and may be a better survival estimator than the CJS model. We feel that Burnham's combined analysis provided the best survival estimates since it included the greatest amount of data for survival estimation. Since dead returns are a factor in the model, behavioral differences during capture (i.e. trap shyness) are not relevant. Survival estimates referred to in the remaining discussion are from Burnham's combined model.

Known fate survival estimates may be biased high for 1-and 2-year-old males since 3 1-year-olds and 4 2-year-olds prematurely lost their ear tag transmitters, and we censored them from the analysis in the month preceding their harvests. This may

partially explain the higher survival rates for yearling males in the known fate model than for the 3 mark-recapture models. However, 2-year-old male survival from the known fate was most similar to the dead recoveries model (lowest estimate for 2-year-old males), and if the prematurely dropped transmitters were accounted for in the known fate model, the survival estimate would likely be the lowest among 2-year-old male survival estimates. Sample sizes for radio-transmitted yearling and subadult bears are smaller than for the marked population (e.g. ear tags and tattoos) and may not be as representative.

We found 2 reported yearling survival rates from hunted populations in the literature; one in Alaska where a combined analysis of yearling males and females had survival rates of 0.75 (Schwartz and Franzmann 1992), and another in Oregon where a life table analysis provided estimates of 0.71 for males and 0.76 for females (Lindsey and Meslow 1980). Our estimate of 0.87 is higher than both estimates of yearling female survival, and our estimate of 0.32 is lower than both estimates for yearling male survival. We can not explain the differences in yearling survival rates between this study and the estimates from Oregon and Alaska, but differences may stem from hunter preferences, bear sizes, nutrition, state game regulations, and differences in movement and dispersal patterns among black bear populations.

Reported survival rates of subadult bears often are lower than adult bears (Schwartz and Franzmann 1992, Beringer et al. 1998), and most studies report lower survival for subadult males than subadult females in hunted populations (Bunnell and Tait 1981, Schwartz and Franzmann 1992, Beringer et al. 1998, Klenzendorf 2002). Our survival rate estimate of 0.87 for 2- and 3-year-old females is similar to earlier estimates

in western Virginia (0.80; Klenzendorf 2002) and eastern Virginia (0.87; Hellgren 1988). Reported survival rates for subadult female black bears in North America range between 0.53 and 0.93 for hunted populations; our estimated survival rate fell within reported estimates (Table 8). Annual survival for subadult males was 0.59, similar to the 0.52 reported earlier by Klenzendorf (2002) for the same area, but much lower than the 1.00 for subadult males reported for the lightly hunted bear population in the Great Dismal Swamp National Wildlife Refuge in eastern Virginia (Hellgren 1988). Our estimate was similar, but slightly higher, to other reported survival estimates (0.27 - 0.52) for subadult males in hunted North American black bear populations (Table 8).

One-, 2-, and 3-year-old females survived better than males in all age classes, respectively. Female survival appeared to be fairly constant from age 1 through 3 (approximately 0.90), while male survival was lower for all age classes. Yearling males appeared to have increased survival after age 1, but did not reach the high levels of female survivorship during their subadult age classes. If cub sex ratio is 1M : 1F, as here in Virginia (Klenzendorf 2002), and fewer subadult males survive to adulthood, the adult sex ratio should favor females. Females become reproductively active at age 3 or 4 in Virginia (Klenzendorf 2002), and have the opportunity to add to the population. High survival of subadult females is likely contributing to the apparent increase in Virginia's black bear population (Martin and Steffen 2000, Klenzendorf 2002).

Two- and 3-year-old females and 1- and 2-year-old males appeared particularly vulnerable to hunting with hounds according to known fate survival analysis by hunting method (Tables 1 and 2). Yearling females ($S = 0.90$) may not be as at risk as other age and sex groups, since Virginia law requires that harvestable bears weigh 45.4 kg.

Table 8. Annual survival rates for subadult (2- and 3-year-olds) black bears in North America.

State	Status	Female	Male	Estimator	Citation
Virginia	Hunted	0.80	0.52	Burnham's combined model	Klenzendorf 2002
North Carolina	Hunted	0.53	0.27	Kaplan-Meier	Beringer et al. 1998
Alaska ^a	Hunted	0.93, 0.66	0.50	Kaplan-Meier	Schwartz and Franzmann 1992
Virginia	Not hunted	1.00	1.00	Heisey-Fuller ^b	Hellgren 1989
Colorado	Not hunted	0.94	0.76	modified Heisey-Fuller	Beck 1991
Coahuila, Mexico	Not hunted	-	1.00	Heisey-Fuller	Doan-Crider and Hellgren 1996

^a Two study areas presented for Alaska.

^b Heisey and Fuller (1985).

Average weight during summer trapping for yearling females ($n = 18$) was 30.8 kg and averaged 42.2 kg by summer as 2-year-olds ($n = 68$). All yearling female mortality was from rifle hunting without hounds. Rifle hunters are believed to be more opportunistic in their harvest since they do not often have the opportunity to assess a treed bear, as do hunters who use hunting hounds (Litvaitis and Kane 1994). Survival rates were lowest for 1- and 2-year-old males during the hunting with hounds season. These age classes may be particularly vulnerable to this method of hunting. However, by age 3, hunters using hounds harvested none of our 4 radio-marked male bears. Possible reasons for an increased survival of 3-year-old male bears, especially during the hunting with hound season, are the scarcity of this age group since many males are harvested as 1- and 2-year-olds, increased ability to avoid hunters, and possible early denning (i.e. October - mid November). Some adult males within our population avoid harvest due to early denning (CABS, unpublished data), and we speculate that some subadult males that survive to adulthood may also exhibit this behavior. Harvested 3-year-old male bears were taken during the archery and rifle only seasons, which occur before hunting with hounds season.

In Virginia, yearling and subadult males accounted for approximately 85% of the total male harvest during the 1978 - 1998 hunting seasons and 43% of the total harvest (Martin and Steffen 2000). Higgins (1997) estimated that during the 1994-1995 hunting seasons in Virginia, 37% of the available subadult male population was harvested. Increased movements during dispersal, larger home ranges, and inexperience in avoiding hunters probably contribute to the high mortality rate of subadult males. Mortality of the dispersing cohort is often attributed to closer contact with hunters and roads. In Alaska,

17 of 18 dispersing males died close to roads or river access areas (Schwartz and Franzmann 1992).

MANAGEMENT IMPLICATIONS

We do not believe that the low survival rate of yearling and subadult males is a cause for concern in Virginia. Adult female survival has been identified as the most influential demographic parameter in maintaining black bear population levels (Eberhardt 1990). Virginia's black bear population appears to be stable or increasing, at a time when total harvest is increasing (Martin and Steffen 2000), and the reproductive rate of adult females is high (Klenzendorf 2002). Harvest of adult females may stay at moderate to high levels (e.g. 10 -15 % of the harvest, respectively; McLaughlin 1998) without harm to the overall population level due to the harvest of a larger population of subadults. However, Miller (1990) cautioned against using age composition in the harvest as a bear management tool (Miller 1990) since harvest composition does not necessarily reflect population composition. Harvest composition may be influenced by hunter biases and differential vulnerability to harvest of bears of different sex and age (Bunnell and Tait 1980). Also, in the promiscuous mating system of black bears (Rogers 1987), few subadult males needed to reach adulthood to breed many receptive females in an area. As the Virginia black bear population appears to be growing, subadult male bears appear to be a surplus for harvest.

Survival estimates from this study could be used to assist in the management of Virginia's black bear population. Of particular use to biologists and managers are subadult survival estimates by each method of harvest. Manipulation of the length of

archery, rifle season, and hunting with hounds seasons likely would result in increased or decreased harvest of subadult bears with increased or decreased season length, respectively. Current survival estimates, along with harvest totals, could be used to predict the level of harvest under various season lengths in order to achieve specific management goals through the harvest of subadult bears.

Many researchers present survival of the subadult age class instead of a further breakdown by age (Beck 1991, Schwartz and Franzmann 1992, Beringer et al. 1998). Pooling of subadult bears into one age class (i.e. subadults) may be an appropriate way to estimate survival for 2- and 3- year-old black bears. Most parsimonious models for all mark-recapture analyses combined 2- and 3-year-old males and females as having the same survival probability. Pooling of 2- and 3-year-olds provides for greater sample size and may have greater ease of use for bear managers. However, we recommend that survival be estimated separately for 2- and 3-year-olds before pooling since survivorship in other black bear populations may be influenced differently by local variables such as harvest regulations, dispersal, nutrition, etc.

Few studies use mark recapture data to estimate survival for black bear populations even though most of the necessary data are collected to conduct such analyses. Our survival estimates from mark-recapture models were lower than estimates from the Kaplan - Meier analysis. However, more accurate survival estimates may be derived from the larger, and more representative, marked sample. With careful attention paid to assumptions, researchers may find they can gain better estimates from mark - recapture analysis with use of programs such as MARK. This may be particularly true, if hunter harvest biases are known to exist for radio-transmitted bears.

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CHAPTER 3: BLACK BEAR FAMILY BREAKUP IN VIRGINIA

ABSTRACT

Family breakup is an important event in the life history of black bears, marking the initial dispersal and home range construction of yearling bears, and perhaps marking the timing of estrus and breeding opportunities for adult females. We monitored 6 black bear family groups with 12 yearlings (6M : 6F) to determine the timing of family breakup; we intensely monitored 3 of the family groups to document home range establishment and movements by 5 subadult bears (2M : 3F) following separation from their mothers. Estimated dates of family breakup were 28 May and 2 June. Family breakups occurred before peak dates of estrus on our 2 western Virginia study areas. We detected 1 reassociation between a mother and her yearling offspring. Following family breakup, female yearlings ($n = 3$) remained within or near their mothers' home range while subadult males ($n = 2$) dispersed. All yearlings ($n = 5$) shared $\geq 50\%$ of post-breakup home range with their mothers.

INTRODUCTION

The timing of family breakup is poorly documented in North American black bear populations (Clevenger and Pelton 1990, Schwartz and Franzmann 1992). Studying family breakup and the dissolution of the bond between adult female bears and their offspring requires monitoring the entire family group. However, many bear studies neglect collaring cubs and yearlings because their fast growth rates increase the risk of collar related neck injuries. In addition, it is difficult to capture, monitor, and locate dispersing individuals following breakup events. Thus, rarely are estimated dates of family breakup obtained for black bear populations.

Identifying when family bonds dissolve may clarify the relationship between family dissolution and the onset of estrus in females, and may help pinpoint when dispersal begins for subadult bears. Breakups of black bear families occur during the months of May – July in North America (Jonkel and Cowen 1971, Reynolds and Beecham 1980, Rogers 1987, Clevenger and Pelton 1990, Schwartz and Franzmann 1992). Adult females normally provide parental care for approximately 16-17 months (Rogers 1987), but may provide care for up 29 months (Jonkel and Cowan 1971). Family bonds appear to weaken over time as subadult female offspring develop a home range within the adult female's home range and subadult male offspring disperse (Rogers 1987, Schwartz and Franzmann 1992).

The Cooperative Alleghany Bear Study began focusing on the dynamics of family breakup during the 2000 field season. Specific objectives of this study were to determine the mean date of family breakup in western Virginia, determine if reassociations occur between family members following family breakup, determine if the timing of family

breakup coincides with onset of estrus, and determine differences between male and female offspring in post-breakup home range use.

STUDY AREAS

The Cooperative Alleghany Bear Study has 2 study areas in western Virginia separated by approximately 140 km (Figure 1; Chapter 1). The 860-km² northern study site in the George Washington-Jefferson National Forests is centered in Augusta and Rockingham Counties. The site contains portions of the Dry River and Deerfield Ranger Districts in the Ridge and Valley Province of the Appalachian Mountains. Elevations range between 488m along the base of Little North Mountain and 1,360m at the top of Elliott Knob (Kozak 1970).

The 1,540-km² southern study site, also located in the George Washington-Jefferson National Forests, encompasses much of Montgomery, Giles, and Craig counties. The study site is in the Blacksburg and Newcastle Ranger Districts in the Ridge and Valley Province of the Southern Appalachian Mountains (United States Department of Agriculture, 1965). Elevation ranges from 492m along the Craig Creek drainage to 1,378m at Mountain Lake.

At Dale Enterprise in the adjacent Shenandoah Valley, the average temperatures vary between 0.3 °C and 22.9 °C over the year, with an average of 11.8 °C. Average yearly precipitation is 86 cm and occurs mostly between April and September. Average snowfall is 71 cm/year. The mountains of the study area usually receive more precipitation and average 2.8-5.6 °C cooler than in the Shenandoah Valley (Rawinski et al 1994).

Vegetation in both study sites is similar. Forest cover types on the study areas include: eastern hemlock (*Tsuga canadensis*), sugar maple-beech-yellow birch (*Acer saccharum*, *Fagus grandifolia*, *Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak-black oak-northern red oak (*Q. alba*, *Q. velutina*, *Q. rubra*), northern red oak, yellow poplar-white oak-northern red oak (*Liriodendron tulipifera*), eastern white pine (*P. strobus*), and barren and brush cover such as mountain laurel (*Kalmia latifolia*) or scrub oak (*Q. ilicifolia*) (Rawinski et al. 1994).

METHODS

Fieldwork was conducted during January 2000 - December 2001. We trapped bears during June - August each year with spring-activated Aldrich foot snares and culvert traps, and we entered the dens of radio-collared bears during January – March each year. We used a 2:1 mixture of ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (Rompun, Bayer Corporation, Shawnee Mission, KS; concentration of 300 mg/ml) at a dosage rate of 1cc/45.4 kg (100 lbs.) of body weight to immobilize bears. Drug was administered with a Capchur gun (Palmer Chemical Company, Douglasville, GA) or jab stick. We took standard body measurements, drew blood samples, and extracted a tooth for age estimation (Willey 1974). After all handling was complete, Antagonil (yohimbine hydrochloride, Wildlife Laboratories, Incorporated, Fort Collins, CO; concentration of 5 mg/ml) was administered at a dosage of 2cc/45.4 kg as an antagonist to the xylazine hydrochloride.

We attempted to enter the dens all radio-collared females denning with yearlings during the 2000 and 2001 den seasons. We placed ear tag transmitters (Advanced Telemetry Systems, Ins., Isanti, MN [ATS]) with mortality switches on all yearling black bears handled in the den to avoid the potential for collar related injuries. We attempted to monitor all individuals from each family group from den emergence through denning the following winter.

Ground telemetry using Telonics (Telonics, INC., Mesa, AZ) receivers and H-antennas was conducted along an extensive station system established along forest roads and trails. We located adult females weekly from the ground during January 2000 - December 2001, and located their yearlings with similar frequency from the estimated time of family breakup through den season. We walked in on ear tag transmitters emitting mortality signals to determine cause of death or to retrieve dropped transmitters. Bearing error, estimated with a beacon study, was ± 14 degrees. Therefore, azimuths taken at 1 km, 1.5 km, and 2 km from the bear could be 249 m, 374 m, and 498 m from the correct location, respectively. We conducted aerial telemetry approximately every 28 days to locate missing bears and supplement ground telemetry.

We used 481 triangulations from a random sample of 35 radio-transmitted bears to define acceptable triangulations for home range analysis based on error ellipse size. Error ellipses had a mean of 18 ha, median of 8 ha, and ranged from 0 to 394 ha. We eliminated the upper 5% of error ellipses, which coincided with acceptable triangulations having error ellipses of ≤ 67 ha.

Bears became one year older upon emergence from their winter dens or on 15 January, if they did not den. Telemetry data for those individuals that spanned >1 year was apportioned by age class.

Date of family breakup was estimated by (1) monitoring family groups, and (2) locating family members. To estimate date of family breakup with monitoring data, we examined records kept by the person doing the monitoring of whether yearlings were judged to be with their mothers. Judgments were based on common direction and strength of transmitter signal for all family members. Estimation of family breakup date with monitoring data was used for all families since triangulations often could not be obtained.

To estimate date of family breakup with location data, we compared locations of all family members taken on the same day within a 1-hour time period. We attempted to locate the entire family group at least once a week. Yearling black bears separated by >500 m were considered to have separated from their mothers. For both methods, date of family breakup was estimated as the midpoint between the last day the group was monitored/located together and the first day family members were monitored/located separate from one another. Estimated family breakup dates of individual families were converted into the day of the year and averaged.

We examined the dissolution of family bonds by calculating the monthly mean distance between paired locations of adult females and their yearlings, and between siblings after family breakup until denning. Locations were paired only if the locations were collected on the same day. Standard deviations were calculated for all mean distances.

Reassociations are reported as the dates at which we monitored 2 individuals of a family group together following a breakup event. We possibly missed some reassociations due to the inability to monitor bears daily, and we did not conduct telemetry at night.

Home ranges and home range overlap for each family group were analyzed with ARC-View Version 3.1 with animal movements and x-tools extensions. We computed fixed kernel home ranges with 95% probability contours for adult females and yearlings (Worton 1989). Bandwidth (i.e. smoothing parameter) was selected by the animal movement extension. Fixed kernel applies the same bandwidth over the entire evaluation area and is known to produce more accurate estimates of outer contours of the home range (Worton 1995). We selected fixed kernel estimators for home range analysis for the following reasons: requires only 30 locations to calculate home range, is free of distribution assumptions, is a nonparametric methodology, is not sensitive to outliers, and allows for multiple centers of activity (Kernohan et al. 2001). We used only locations obtained after family breakup to construct yearling home ranges. We did not estimate seasonal home ranges because our sample sizes were small.

RESULTS

Marking Family Groups

2000. We suspected 20 radio-collared females on the northern study site had yearlings with them in the dens during the 2000 den season. However, several of these dens were not entered for the following reasons: the adult female was alone ($n = 4$), the adult female had cubs instead of yearlings ($n = 2$), the den was unsafe to enter ($n = 4$) (Godfrey et al.

2000), position of the adult female in the den made darting unsafe ($n = 2$), or the family ran upon our approach ($n = 4$). We successfully entered 4 dens consisting of 3 adult females and 10 (3M : 7F) yearlings; 1 female fled the den and was not captured (Table 9). All yearlings received an ear tag transmitter during den work. One additional adult female, 402, and her female yearling, 544, were in a den unsafe to enter. The yearling was wearing an expandable collar from the previous season (i.e. collared in the den as a cub), which remained operative through family breakup, thus the family was entered into the analysis.

We suspected 3 adult females on the southern study area to have yearlings. One of these females did not den, but did not have yearlings with her when treed in early April. We successfully entered dens of the 2 remaining adult females and their 5 (5M: 0F) yearlings (Table 9). All but 1 yearling, male 10231, received an ear tag transmitter during den work.

On the northern study site, circumstances developed in many family groups that hampered obtaining family breakup dates (Table 9). Female yearling 576 died sometime after we left the den of adult female 299. The yearling was removed from further analysis. Adult female 187 eluded capture at the den site and never rejoined her 2 yearlings after handling was complete. The 2 yearlings remained at the den site for approximately 2 weeks then separated from one another. The family was eliminated from family breakup date analysis. The family group of adult female 199 (yearlings 670, 671, and 672) experienced an unknown event during mid-April that separated the adult female and all 3 yearlings from one another. Yearlings 670 and 671 were last heard on 27 and 19 April, respectively. Yearling 672 rejoined with its mother by 27 April.

Table 9. Family groups of radio-collared adult female black bears whose dens were entered in the George Washington-Jefferson National Forests, Virginia, 2000.

Mother	Yearling	Sex	Comments
165	564	F	Yearlings 565 and 566 dropped transmitters on 7 June and 5 June 2000, respectively.
	565	F	
	566	M	
187	567	M	Mother separated from yearlings during den handling and never rejoined. Removed from family breakup date analysis.
	570	F	
199	670	F	Family experienced some breakup event in mid-April. Yearlings 670 and 671 did not rejoin the family group.
	671	F	
	672	M	
299	575	F	Yearling 576 died shortly after handling in the den.
	576	F	
402 ^a	544	F	Yearling 544 wore a cub collar through family breakup.
10041	10230	M	Transmitter not attached to yearling 231.
	10231	M	
	10232	M	
10047	10217	M	Adult female dropped collar after den handling. Believed to still be with yearlings through breakup
	10229	M	

^a Unsafe to enter den of adult female 402. Added to study since yearling wore functioning cub collar.

On the southern study site, adult female 10047 dropped her collar after handling at the den was complete, but was assumed to still be with her 2 radio-marked yearlings. Her yearlings remained at the den site the remainder of the den season, and the adult female's collar was found at the den site after the family left their den area. It seems likely that had the adult female abandoned the yearlings at the den site after handling, the yearlings would have followed her or left the den. Date of breakup for the yearlings was used as the date of breakup for the entire family since we were unable to detect any siblings remaining together after leaving their mother's for any other family.

2001. We suspected 5 radio-collared females on the northern study site had yearlings with them in the dens during 2001 den season. In addition, we attempted to enter the den of a lone yearling whose mother was harvested during the 2000-2001 bear season. We did not enter 4 of the 5 dens because the adult female had cubs instead of yearlings ($n = 1$), the den was unsafe to enter ($n = 1$), position of the adult female made darting unsafe ($n = 1$), or the family ran upon our approach ($n = 1$). We entered the den of the remaining adult female and captured her and a female yearling while 2 yearling males left the den site and eluded capture. The adult female and yearling female separated 2 days after our den visit and did not rejoin. The family group was eliminated from further analysis.

We suspected 2 adult females on the southern study area to have yearlings with them in the den, but neither female had yearlings when the den sites were investigated. Thus, no family groups were added to the breakup analysis for 2001 from either study site.

Date of Family Breakup

No yearlings (n = 10) retaining their radio transmitter through family breakup of any family group (n = 6) were located with other siblings following family breakup. Individual family groups appeared to dissolve in a single day. We estimated 28 May (range 7 May - 12 June) as the mean date of family breakup based on monitoring records for 6 family groups (Table 10). We estimated 2 June (range 18 May - 10 June) as the mean date of family breakup of 4 adult females and their offspring using location data (Table 11). The 2 southern family groups were unusable for estimation with location data since few locations were collected, family members were not located often on the same day, and large error ellipses made it unclear when family members were together and not.

Dissolution of Family Bonds

Family members appeared to become separated by greater mean distances over time (Table 12), although sample sizes were small for each month. Yearling females were closer to their mothers than yearling males during all months following separation except in June. Maximum mean separation distance for yearling females and males was 1.3 ± 0.7 km during October and 10.9 ± 5.8 km during September, respectively.

Reassociations

Yearling 564 rejoined adult female 165 during 18 - 23 June and on 30 June. No reassociations were recorded between siblings of any families.

Table 10. Estimated dates of family breakup based on monitoring^a of black bear family groups on the George Washington-Jefferson National Forests, Virginia, 2000. Dash signifies date not established.

Adult female	Age	Yearling	Sex	Last date together	Date separated	Estimated Breakup
165	8	564	F	6/1	6/6	6/4
		565	F	6/1	6/6	6/4
		566	M	6/1	-	-
199	6	670	F	-	-	-
		671	F	-	-	-
		672	M	6/10	6/13	6/12
299	11	575	F	5/5	5/8	5/7
402	6	544	F	5/31	6/1	6/1
10041	11	10230	M	5/22	5/28	5/25
		10231	M	-	-	-
		10232	M	5/22	5/28	5/25
10047	9	10217	M	5/28	6/3	5/31
		10229	M	5/28	6/3	5/31

^a Dates estimated by monitoring are the best judgment of field personnel of whether the family group was all together or separated when triangulations were not possible for some or all of the family members.

Table 11. Estimated dates of family breakup based on locations^a for black bear family groups in the George Washington-Jefferson National Forests, Virginia, 2000.

Adult female	Age	Yearling	Sex	Last date together	Date separated	Estimated breakup
165	8	564	F	6/1	6/18	6/10
		565	F	6/1	-	-
		566	M	6/1	-	-
199	6	670	F	- ^b	-	-
		671	F	-	-	-
		672	M	6/1	6/19	6/10
299	11	575	F	5/11	6/27	6/4
402	6	544	F	5/4	6/1	5/18

^a Dates estimated by location data are based on the triangulation of all family members taken on a single day within 1 hour.

^b Dashes indicate dates not determined.

Table 12. Mean distance \pm SD (km) between same day radio-locations of adult females and yearlings and between siblings after family breakup^a, George Washington-Jefferson National Forests, Virginia, 2000. Number of locations used for estimate in parentheses.

Month	Females and all yearlings		Females and yearlings				Siblings	
			males		females			
June	0.8 \pm 0.4	(11)	0.5 \pm 0.3	(3)	0.9 \pm 0.5	(8)	1.0 \pm 0.3	(3)
July	1.4 \pm 1.3	(12)	1.7 \pm 2.1	(5)	1.2 \pm 0.5	(7)	2.1 \pm 1.3	(2)
August	1.4 \pm 1.3	(14)	2.1 \pm 1.5	(7)	0.7 \pm 0.4	(7)	1.1 \pm 0.9	(6)
September	6.1 \pm 6.8	(11)	10.9 \pm 5.8	(6)	0.5 \pm 0.4	(5)	2.6 \pm 0.0	(1)
October	1.6 \pm 0.7	(5)	2.1 \pm 0.5	(2)	1.3 \pm 0.7	(3)	-----	(0)
November	2.1 \pm 2.6	(4)	3.4 \pm 3.7	(2)	0.9 \pm 0.1	(2)	-----	(0)

^a Mother and yearling pairs are from six families.

Home Range Size and Overlap

Three family groups consisting of adult females plus 2 yearlings, 2 yearlings, and 1 yearling, respectively, had individuals with enough locations to estimate home range size and overlap (Table 13). Home ranges of the 3 adult females ranged from 3.9 – 14.3 km². Mean yearling home range size (n = 5) after family breakup was 13.5 km² and ranged from 5.4 – 22.1 km² (Table 13). Overlap between adult females and their yearlings ranged from 54.9- 90.3 %.

Individual Accounts of Post Breakup Movements

Family Group 165. Family group 165 consisted of adult female 165, female yearlings 564 and 565, and male yearling 566 (Figure 2). Female yearling 564 was regularly located inside her mother's home range following family breakup. She moved 5.1 km north of her mother's home range in November, but returned to her mother's home range in December and denned inside it. Her transmitter died during the den season. She was trapped in June and July 2001 as a 2 year old inside the western edge of her mother's home range. Remote cameras recorded 5 pictures of her at an area close to the center of her mother's home range during August 2001. It appears that she may have established her home range within her mother's home range.

Female yearling 565 dropped her ear tag transmitter on June 5, 2000 just before the estimated date of family breakup for the rest of the family, thus we failed to identify her home range. However, we trapped her in July 2001 as a 2 year old inside her mother's home range. Remote cameras recorded 2 pictures of her during August 2001 and 5 pictures during October 2001; all were at locations inside the mother's home range. It appears that she may have established a home range within that of her mother's.

Table 13. Fixed kernel home range sizes and percent overlap of mother/yearling home ranges for selected family groups of black bears on the George Washington-Jefferson National Forests, Virginia, 2000.

Bear Id	Sex	N ^a	Period monitored	Home range (km ²)	Overlap ^b (km ²)	Overlap (%)
165 ^c	F	89	03/99- 03/01	9.3	-	-
564	F	45	06/00- 08/01	9.2	5.4	58.1
566	M	15	06/00- 10/00	22.1	8.4	90.3
566 ^d	M	05	07/01- 09/01	14.5	0.0	0
187 ^c	F	78	03/99- 03/01	14.3	-	-
567	M	37	02/00- 01/01	13.3	7.3	54.9
570	F	20	02/00- 10/01	17.6	9.9	56.3
299 ^c	F	45	01/99- 06/01	3.9	-	-
575	F	29	06/00- 10/01	5.4	3.0	76.9

^a N = number of locations.

^b Overlap is computed as the amount of home range (km²) shared by the home ranges of yearling and his/her mother.

^c Adult female with yearling offspring in following rows.

^d Summer 2001 home range based on trapping and remote camera locations.

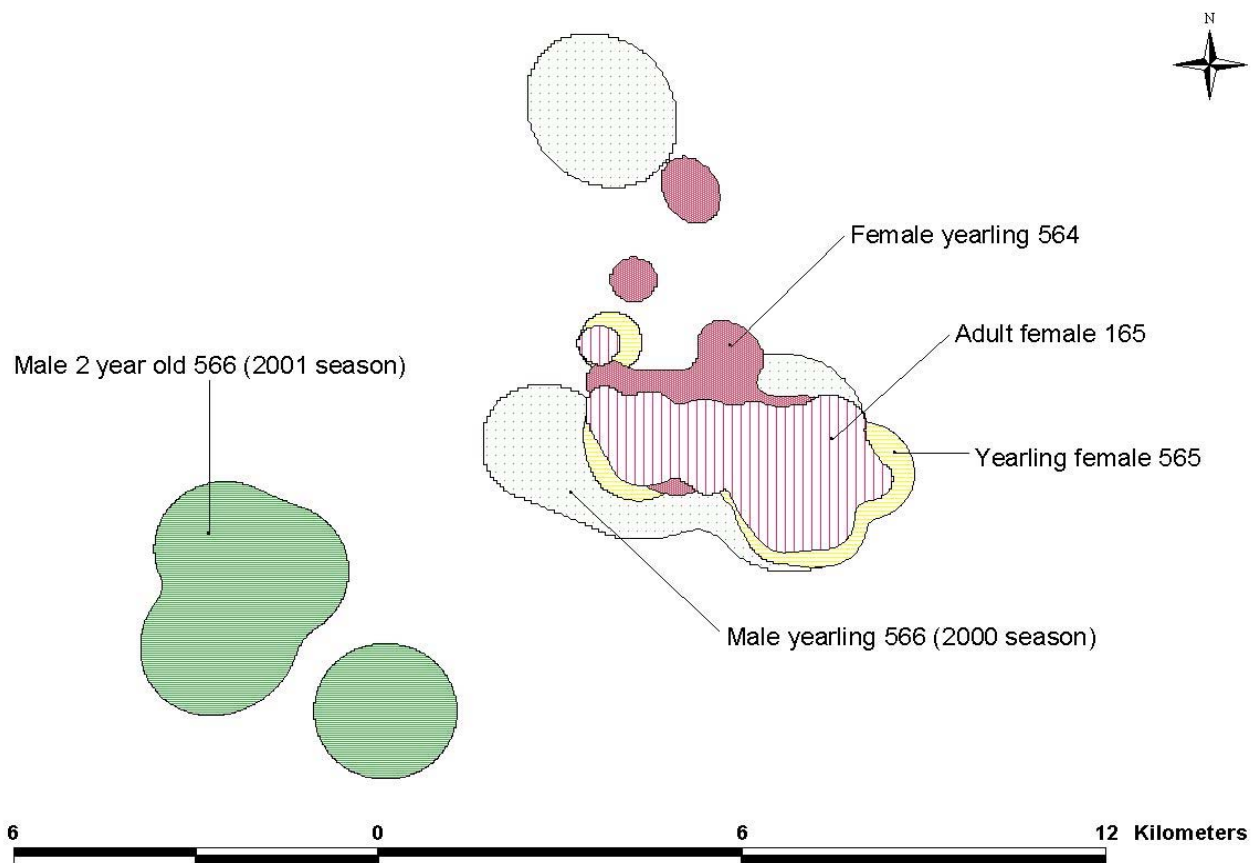


Figure 2. Home ranges and home range overlap of family group 165 estimated with the fixed kernel method on the George Washington-Jefferson National Forests, Virginia, 2000-2001.

Male yearling 566 ranged widely over his mother's home range after family breakup, covering over 90% of her home range. He left her home range in October 2000 and was located 7.2 km due north of the center of his mother's home range twice during the month. He dropped his ear tag transmitter on October 17. In June 2001 he was trapped approximately 8.3 km to the southwest of his mother's home range.

Additionally, he was trapped at 2 more trap sites in the same area later in June. During August 2001, remote cameras in the same area as the trap sites recorded him twice. It is possible that this may be his new home range.

Family Group 187. Family group 187 consisted of adult female 187, male yearling 567, and yearling female 570 (Figure 3). The family was separated at the den site during February 2000, and the adult female did not rejoin her yearlings after separation. Male yearling 567 and female yearling 570 stayed in their mother's home range following the separation and through the summer. Male yearling 567 left his mother's home range in mid October and moved northeast approximately 5.4 km before returning the next week. In late October he moved again to the same general area about 5.0 km from his mother's home range and remained and denned. The ear tag transmitter failed during den season, and we have not recaptured him. It is unclear if the bear continued to move as a two year old or if this was his new home range.

Female yearling 570 dropped her ear tag transmitter in July 2000. She was recaptured inside her mother's home range in July 2001 as a 2-year-old. Remote cameras recorded her 6 times in August and once in October 2001. Two of the remote camera sites put her at 1.1 km and 0.4 km outside the western edge of her mother's home range,

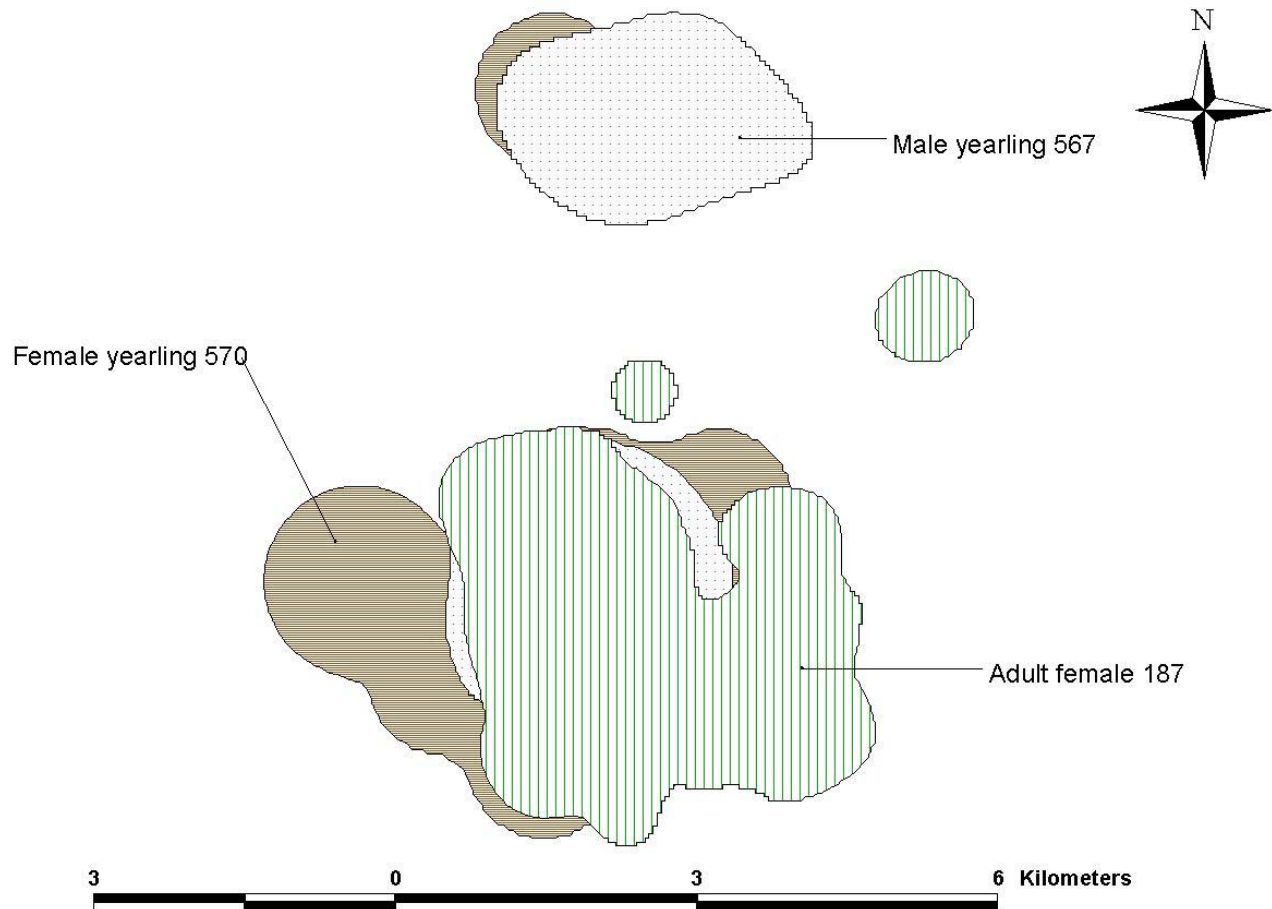


Figure 3. Home ranges and home range overlap of family group 187 estimated with the fixed kernel method on the George Washington-Jefferson National Forests, Virginia, 2000-2001.

while the rest were inside her mother's home range. The yearling may have set up a home range adjacent to and/or inside her mother's home range.

Family Group 299. Family group 299 consisted of adult female 299 and yearling female 575 (Figure 4). Female yearling 575 stayed almost entirely within her mother's home range through denning as a yearling. The area in which she and her mother established home ranges was remote and difficult to acquire telemetry readings. Yearling 575 was trapped as a 2 year old in June 2001 inside her mother's home range. Remote cameras recorded 1 picture of her in August 2001 and 2 in October 2001 on the southwest corner of her mother's home range. It appears that she may have established her home range within or adjacent to her mother's home range.

DISCUSSION

Date of Family Breakup

Adult females provided parental care to their offspring for 17 - 18 months before family breakup events in May and June. Similarly, female black bears in Minnesota provided parental care for 16 - 17 months (Rogers 1987). No radio collared adult female in this study provided care for >2 years as reported by Jonkel and Cowan (1971) in Montana.

Approximately 90% of our triangulations were taken at less than 1.5 km (error \pm 374m), so we felt we accurately detected family breakups using location data (i.e. separation of 500 m between mother's and their offspring). Our estimated mean dates of family breakup (28 May - monitoring data; 2 June - location data) were similar to estimates from other North American black bear populations (Alt 1978, Rogers 1987, Clevenger and Pelton 1990, Schwartz and Franzmann 1992). Most black bear families in

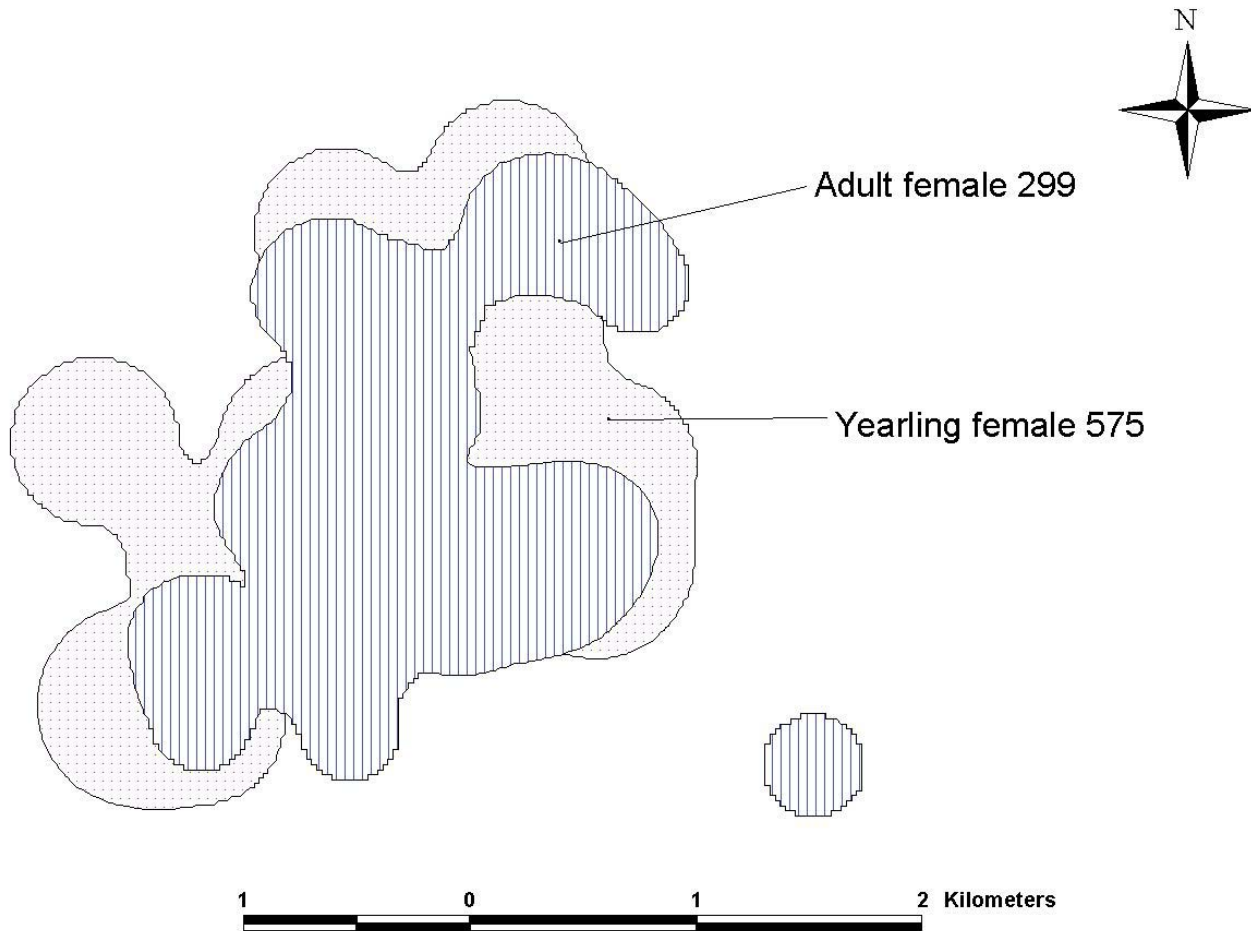


Figure 4. Home ranges and home range overlap of family group 299 estimated with the fixed kernel method on the George Washington-Jefferson National Forests, Virginia, 2000-2001.

this study separated between the last week of May and mid June. Our earliest family breakup (7 May) was unlike the rest of our family groups, yet not unlike the earliest breakup dates reported in populations in Alaska (8 May; Schwartz and Franzmann 1992) and Pennsylvania (10 May; Alt 1978). Since we were not able to monitor and locate family groups daily, our estimated dates likely do not reflect the precise date of breakup. The subjective nature of the decisions for estimating family breakup date with monitoring data may make this estimate less precise, but our 2 estimates were similar (within 4 days).

In Minnesota, Rogers (1987) reported that all family groups (n = 28) separated between late May and 3 July. In Tennessee, Clevenger and Pelton (1990) reported 2 family groups separated between 29 May - 5 June and 22-25 June, respectively. Alt (1978) reported 5 family breakups in Pennsylvania occurred in May and 1 in June. In Montana, 2 family groups separated in late June and early July (Jonkel and Cowan 1971). In Idaho, Reynolds and Beecham (1980) reported 4 family groups dissolved between 24 May and 4 June.

Reasons for variation in the timing of family breakups are not clear. Rogers (1987) concluded that the mother prompts family breakup since all, or most, yearlings leave at the same time in most cases. Sudden social intolerance by the adult female for her yearlings (Rogers 1977), or by adult males during the breeding season (Herrero and Hamer 1977), is thought to be responsible for family breakups. Ternent and Garshelis (1998) reported an observation of a family breakup instigated by a male bear. The male's presence apparently triggered the adult female to become hostile towards her yearlings. The beginning of the breeding season in Minnesota (Rogers 1977) and Tennessee (Eiler

et al. 1989) occurred after the earliest dates of family breakup (Rogers 1977, Clevenger and Pelton 1990). This suggests that mothers may force the family to breakup prior to coming into estrus.

Reproductive status has been ascertained by measuring hormone levels in the blood of bears (Foresman and Daniel 1983; Tsubota et al. 1987; Palmer et al. 1988; Hellgren et al. 1990; Derocher et al. 1992) and other mammals (Weber et al. 1982; Woods et al. 1986). However, after an extensive literature review, we were unable to find research concluding that changing hormone levels in reproductively active mammals are the mechanism for family dissolution. It is unclear to what extent family breakup is encouraged by hormonal changes associated with estrus in adult female bears, or if an environmental cue, rather than a physiological one, may be the mechanism for family dissolution. We speculate that hormonal changes associated with the onset of estrus are responsible for family breakup. Research into this connection is problematic due to a lack of clear definitions of when a family unit has dissolved for most mammals, and an inability to regularly measure hormone levels before, during, and after family breakup events.

Several endocrine hormones play an important role in preparing a bear for estrus and pregnancy, including progesterone, oestradiol, luteinizing hormone, and prolactin (Tsubota et al. 1998). If adult females indeed initiate family breakups, it may be a hormonal response due to increases or decreases in hormones at the onset of estrus. Prolactin levels in female black bears increased sharply in Minnesota between March and their peak in June when oestradiol levels were also at their highest levels (Tsubota et al.

1998). While the implication is that hormonal shifts may be responsible for such a behavioral mechanism, further study is needed to confirm or reject this hypothesis.

Family breakups apparently coincide with the breeding season in black bears. In Alaska, the breeding season occurred from mid-May to early July and yearlings left their mothers prior to, or during, this season (Schwartz and Franzmann 1992). The earliest separation (n = 28 family groups) was 8 May and all separated by 25 June (mean = 2 June). In Virginia, Echols (2000) reported adult females displayed signs of estrus between 6 June and 22 August. Mean date of estrus was 16 July, while the majority of females exhibiting signs of estrus were captured between 15 June and 31 July. Our dates of family breakup in May and early June support the idea that mothers separate from their offspring before the onset of estrus. Variation in the date of individual family breakup may be due to differences in timing of hormone releases during the onset of estrus in female black bears.

Similar to other studies, families in our study appeared to dissolve suddenly, and family groups did not experience straggling yearlings (Rogers 1987, Schwartz and Franzmann 1992). No relationship between age of the adult female or litter size and date of family breakup was apparent, although not enough family groups were observed to test statistically. Schwartz and Franzmann (1992) were unable to find statistical differences between litter size and date of family breakup for 18 black bear families in Alaska, although a trend was noted that smaller families broke up slightly earlier.

Dissolution of Family Bonds

If the distance between mother and her offspring over time is an indicator of the strength of family bonds, then these bonds appeared to gradually weaken. Yearlings

were located progressively further away from their mothers through September, $x = 6.1 \pm 6.8$ km), but during October and November, mean distance between adult females and all their yearling offspring combined fell to 1.6 ± 0.7 km and 2.1 ± 2.6 km, respectively (Table 12). Distance between male yearlings and their mothers dropped to 2.1 ± 0.5 km in October from a high of 10.9 ± 5.8 km in September. This likely reflects the loss of one dispersing male bear to monitoring and location analysis and the loss of another male to harvest, and not a return of yearling bears to their natal areas.

Clevenger and Pelton (1990) reported that yearlings in Tennessee moved away from their mothers throughout the summer and fall and then, as den season approached, returned to or near the home range of their mother to den. We feel that the number of locations used to estimate mean distances between mothers and offspring in this study are too small to draw conclusions. Yearling females stayed closer to their mothers than yearling males during all months except June, the month of initial family breakup (Table 12). This supports current research suggesting females set up home ranges within or immediately adjacent to the home range of their mothers while males disperse from their mother's home range.

Reassociations

Reassociations of family groups appear to be relatively uncommon after family separation, although the published literature may be somewhat misleading (i.e. most studies, including this one, do not monitor radio-marked bears 24+ hours a day). Within the 6 families monitored in this study, we detected 2 temporary reassociations between one female yearling and her mother in June. Our observations were similar to many other studies that reported few and infrequent reassociations after breakup (Jonkel and Cowan

1971, Rogers 1987, Clevenger and Pelton 1990, Schwartz and Franzmann 1992). In Alaska, reassociations occurred in 2 of 28 family groups. Yearlings in both families rejoined the adult females after breakup and denned with their mothers as 2 year olds. A second family breakup occurred for both families in late May the following year (Schwartz and Franzmann 1992). In Minnesota, Rogers (1987) observed only 1 reassociation within 28 family groups; this reassociation occurred after the mating season in late summer. The family remained together until the following June and then split up. Clevenger and Pelton (1990) detected temporary reassociations for mothers and offspring of 2 family groups and 2 reassociations of sister yearlings. Jonkel and Cowan (1971) reported occasional reassociations between female and offspring and among siblings, but did not report how often. Ternent and Garshelis (1998) reported 2 instances of yearlings rejoining for brief periods of time after family breakup. Reassociations have been reported for both male and female yearlings.

Home Range Size and Overlap

Home range sizes of adult females on our study area in western Virginia were similar to those reported in the literature (Rogers 1977, Reynolds and Beecham 1980, Clevenger and Pelton 1990). Three female yearlings had home range sizes of 5.4, 9.2, and 17.6 km², which is similar to estimated subadult female home ranges of 2.5 - 21.6 km² (mean 9.0 km²; n = 4) reported earlier on our northern study area (Higgins 1997). These also are similar to reported home ranges of yearling black bears in Minnesota (n = 24; 1 – 7 km²; Rogers 1977) and Idaho (n = 10; 5 – 9 km²; Reynolds and Beecham 1980). Yearling home ranges in Virginia following family breakup were smaller than the mean yearling home range in Tennessee (30 km²), although home range size there may have

been inflated by the inclusion of long distance fall movements by 3 of 6 yearlings (Clevenger and Pelton 1990).

In Tennessee, summer home ranges were greater for adult females than for yearlings; however during the fall, many of the yearlings left their mother's home ranges and established larger home ranges than those of the adult females (Clevenger and Pelton 1990). We were unable to construct seasonal home ranges for our yearling bears due to low number of locations during individual seasons, but for our 3 family groups that were intensely analyzed, we found that 3 (1M : 2F) of 5 (60%) yearlings had larger home ranges than their mothers.

Home range overlap between yearling black bears and their mothers was prevalent following family breakup during this study. All yearlings overlapped at least 50% of their mother's home range. No pattern in percent overlap between male and female yearlings with their mothers' was discernable.

MANAGEMENT IMPLICATIONS

Family breakups are likely to be initiated by adult male or female bears. Hound training season and bear harvest season (i.e. September through December) in Virginia have the potential to separate families earlier while the offspring are between 9 and 12 months old. The frequency of these events is not known, but we have recorded several instances of family breakup during the hound training season. We also have recorded the harvest of females with cubs of the year and have evidence that cubs can den and do survive after these human caused breakups (Cooperative Alleghany Bear Study, unpublished data). If an earlier hound training season is established as proposed in

Virginia, bear hunters could affect family breakups by separating yearlings or cubs earlier than would naturally occur.

The relationship between family breakup and the onset of estrus remains unclear and further data would help contribute to stronger determination of the relationship. This is a fertile area for more in-depth investigation.

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CHAPTER 4: DISPERSAL MOVEMENTS BY SUBADULT BLACK BEARS IN VIRGINIA

ABSTRACT

Dispersal plays an important role in the population dynamics of large carnivores, however dispersal by subadult black bears (*Ursus americanus*) is poorly understood in Virginia and in North America. Thus, during 1999-2002, we studied the movements of 31 (11M : 20F) subadult black bears born on our 2 study areas in western Virginia and 70 (44M : 26F) subadult bears captured during the summer on the study areas. No radio-marked, resident, subadult female bears exhibited dispersal behavior while 3 of 11 (27%) radio-marked, resident, subadult males dispersed ($P = 0.04$). Resident and summer capture male bears moved greater distances than females from yearling den location ($\chi^2 = 8.54, P = 0.01, df = 2$) or summer capture location ($\chi^2 = 22.02, P < 0.01, df = 2$); no female moved > 10 km between initial and final locations ($x = 2.7$ km, range 0.2 - 9.0 km). The greatest subadult male movement was 80 km ($x = 13.4$ km, range 0.6 - 0.80 km), and dispersal movements primarily occurred within the 1 and 2-year-old age classes. Direction of movement between initial and final locations for dispersing bears was not random (Raleigh's $r = 0.56, P = 0.02$); bears appeared to follow the orientation of the predominant ridgelines and avoided leaving the national forest. All mortality of dispersing and non-dispersing bears was due to harvest. Lack of female dispersal may require managers to control local harvest of females providing for continued reproduction and growth within some areas.

INTRODUCTION

Dispersal is one of the least studied demographic parameters in North American black bear populations (Rogers 1977, 1987; Clevenger and Pelton 1990; Schwartz and Franzmann 1992). Dispersal in black bears generally occurs in the subadult age class and primarily by males (Rogers 1987; Schwartz and Franzmann 1992). Subadult bears are capable of traveling long distances (Rogers 1987), which has implications for genetic variability among bear populations, usefulness of bear refuges, and consequences for survival (Clevenger and Pelton 1990). However, many of those conducting black bear studies are reluctant to collar fast growing subadult animals because of the potential for ingrown collars, and because dispersing individuals are difficult to monitor and recapture. Additionally, most black bear studies focus on adult females for reproductive and survival demographics (Eberhardt 1990).

Knowledge of dispersal is important to managers of black bears populations, because of its role in establishing and maintaining black bear populations (Alt 1978). Immigration and emigration of subadult male bears were responsible for maintaining a bear population at a heavily hunted study site in Idaho (Beecham 1980). Dispersal has consequences for bears by bringing them into closer contact with human induced forms of mortality, including harvest and automobile collisions (Schwartz and Franzmann 1992). Schwartz and Franzmann (1992) reported that male black bears were 2-3 times less likely than females to survive to adulthood.

Determining dispersal patterns of subadult bears may aid our understanding of how bears pioneer new areas and locate vacant habitat. Dispersal is critical to reducing the genetic isolation between island populations in Virginia and throughout the

southeastern United States (Hellgren and Vaughan 1989). In addition, dispersing subadult bears may introduce genetic variability into isolated bear populations in Virginia and other states. Determining dispersal patterns may be helpful, and necessary, for building accurate population models for black bears.

The specific objectives of this study were to determine behavioral differences in dispersal between male and female subadult black bears, determine if distance movements varied between sexes, determine the time of year dispersal occurs, determine if bears dispersed randomly, and examine the relationship between dispersal distance and survival.

STUDY AREAS

The Cooperative Alleghany Bear Study has 2 study areas in western Virginia separated by approximately 140 km (Figure 1; Chapter 1). The 860 km² northern study site is located in the George Washington-Jefferson National Forests and is centered in Augusta and Rockingham Counties. The site contains portions of the Dry River and Deerfield Ranger Districts in the Ridge and Valley Province of the Appalachian Mountains. Elevations range between 488m along the base of Little North Mountain and 1,360m at the top of Elliott Knob (Kozak 1970).

The 1,540 km² southern study site is located in the George Washington-Jefferson National Forests and encompasses much of Montgomery, Giles, and Craig counties. The study site is located in the Blacksburg and Newcastle Ranger Districts in the Ridge and Valley Province of the Southern Appalachian Mountains (United States Department of

Agriculture, 1965). Elevation ranges from 492m along the Craig Creek drainage to 1,378m at Mountain Lake.

At Dale Enterprise in the adjacent Shenandoah Valley, the average temperatures vary between 0.3 °C and 22.9 °C over the year, with an average of 11.8 °C. Average yearly precipitation is 86 cm and occurs mostly between April and September. Average snowfall is 71 cm/year. The mountains of the study area usually receive more precipitation and average 2.8-5.6 °C cooler than in the Shenandoah Valley (Rawinski et al 1994).

Vegetation between the study sites is similar. Forest cover types on the study areas include: eastern hemlock (*Tsuga canadensis*), sugar maple-beech-yellow birch (*Acer saccharum*, *Fagus grandifolia*, *Betula allegheniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak-black oak-northern red oak (*Q. alba*, *Q. velutina*, *Q. rubra*), northern red oak, yellow poplar-white oak-northern red oak (*Liriodendron tulipifera*), eastern white pine (*P. strobus*), and barren and brush cover such as mountain laurel (*Kalmia latifolia*) or scrub oak (*Q. ilicifolia*) (Rawinski et al. 1994).

METHODS

Fieldwork was conducted during June 1999 - April 2002. We trapped bears during June - August each year with spring-activated Aldrich foot snares and culvert traps, and we entered the dens of radio-collared bears during January – March each year. We used a 2:1 mixture of ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Fort Dodge, IA) and xylazine hydrochloride (Rompun, Bayer Corporation, Shawnee Mission, KS; concentration of 300 mg/ml) at a dosage rate of 1cc/45.4 kg (100 lbs.) of

body weight to immobilize bears. Drug was administered with a Capchur gun (Palmer Chemical Company, Douglasville, GA) or jab stick. We took standard body measurements, drew blood samples, and extracted a tooth for age estimation (Willey 1974). We attached ear tag transmitters to a sample of subadult bears during the handling process. After all handling was complete, Antagonil (yohimbine hydrochloride, Wildlife Laboratories, Incorporated, Fort Collins, CO; concentration of 5 mg/ml) was administered at a dosage of 2cc/45.4 kg as an antagonist to the xylazine hydrochloride.

We located transmitter-equipped bears using ground and aerial telemetry to determine location and monitor survival. Telemetry locations were collected June 1999 to April 2002. We supplemented ground telemetry with aerial telemetry approximately every 28 days, and we gave priority to bears not found during the ground surveys. Ground telemetry using Telonics (Telonics, INC., Mesa, AZ) receivers and H-antennas was conducted along an extensive station system established along forest roads and trails. We walked in on ear tag transmitters emitting mortality signals to determine cause of death or to retrieve dropped transmitters. Bearing error was found to be ± 14 degrees.

We designated bears 1-year-old as yearlings, 2- and 3-year-olds as subadults, and ≥ 4 years old. We separated radio-marked bears into 2 groups: resident bears, which were known to be born on the study site to a known adult female, and summer captures, which may or may not have been born on the study site. Distance moved for each subadult was calculated as a straight line between initial and final locations. Initial locations were the yearling den site for resident subadults and capture sites for summer captures. Final locations for both groups were transmitter drop sites, harvest sites, or 2002 den sites if the subadult wore its transmitter through the study.

We defined dispersal for male bears as the minimum distance needed to move a subadult male from the center of his mother's home range to an area where he would no longer overlap her home range as he develops his own adult male home range. In our case this was a movement > 18 km between initial and final locations for male subadults, which we arrived at by adding the radius of an average adult female's home range ($x = 2.5$ km) with the diameter of an adult male home range ($x = 15$ km) for our study site.

We constructed 95% fixed kernel home ranges in ArcView 3.2 for resident adult females and their female offspring. Subadult females whose home ranges overlapped with their mother's home range were deemed not to have dispersed. When we were unable to construct home ranges for adult females and their female offspring, we used a movement > 8 km to define dispersal for subadult females. This distance was computed by adding the radius ($x = 2.5$ km) and diameter ($x = 5$ km) of an average adult female home range in our study area. This represents the minimum distance that a subadult female would need to travel to leave from the center of her mother's home range and develop an adult female home range without overlapping her mother's home range.

We conducted a Fisher's exact test to compare behavioral (i.e. dispersal vs. non-dispersal) differences between sexes for resident subadult black bears. We categorized movements by male and female subadult bears into 0-5 km, 5-10 km, and >10 km distance intervals, and used chi-square tests to compare differences in distance moved between sexes within groups (i.e. residents and summer captures), and for each sex between groups. We examined the relationship between summer weight and distance traveled for yearling and 2-year-old males with Pearson's product moment correlation coefficient. We used Rayleigh's test (Batschelet 1981) to determine if direction of

movement was different from random for resident subadults, summer captures, all males moving > 20 km, and all males moving > 15 km. We ran a logistic regression to see if fate (i.e. mortality) of resident and summer captured bears increased with increasing distance traveled for each sex. We also conducted Mantel – Haenszel chi-square tests to determine if mortality risk increased with distance traveled (using 5 km distance intervals) by resident and summer capture subadult male bears. All tests were conducted in SAS (SAS Institute, Inc., Cary, NC), and we used $\alpha = 0.05$ as our significance level.

RESULTS

We attached ear tag transmitters to 31 (11M : 20F) resident and 70 summer capture (44M : 26F) subadult bears. Eleven resident subadult males and 14 resident subadult females were yearlings when outfitted with transmitters; 6 resident subadult females were 2-year-olds when outfitted with transmitters. Twenty-one, 18, and 5 summer capture males and 5, 12, and 9 summer capture females were 1, 2, and 3 years old, respectively, when outfitted with transmitters.

None of 20 resident subadult females exhibited dispersal behavior, while 3 of 11 (27 %) resident males dispersed > 20 km ($P = 0.04$). Nine of 11 (82 %) resident subadult males left their mother's home range. We constructed home ranges for 13 of 20 (65 %) resident subadult females and all continued to overlap their mother's home range. None of the remaining 7 resident subadult females (mother's home range unknown) moved > 8 km from their yearling den site to their final location (i.e. dispersal behavior), thus no subadult female met our definition of dispersal. Summer captures were not analyzed for

dispersal behavior since bears may have moved some distance from their mother's home range before capture.

Resident ($\chi^2 = 8.54$; $P = 0.01$, $df = 2$) and summer captured ($\chi^2 = 22.02$; $P < 0.01$, $df = 2$) subadult males moved farther, respectively, than subadult females in each category. No resident or summer captured subadult female moved >10 km between initial and final locations while 36% of resident and 34% of summer capture males moved >10 km between initial and final locations. We did not detect a difference between resident and summer captured subadult males in distance traveled between initial and final locations ($\chi^2 = 1.21$, $P = 0.547$, $df = 2$); the same was true for subadult females ($\chi^2 = 0.63$, $P = 0.428$, $df = 2$). Yearling and 2-year-old male bears had greater mean distances moved and moved longer distances than 3-year-old males (Table 14). Weight during summer handling was not correlated with distance traveled by yearlings ($r = -0.198$, $P = 0.30$, $n = 29$) or 2-year-olds ($r = 0.044$, $P = 0.87$, $n = 17$).

Direction of travel for dispersing male bears was not different from random for resident males (Raleigh's $r = 0.094$, $P = 0.90$) or summer capture males (Raleigh's $r = 0.184$, $P = 0.24$). Direction of travel was different from random for males that moved > 20 km (Raleigh's $r = 0.596$; $P = 0.02$; $n = 11$) and males that moved > 15 km (Raleigh's $r = 0.513$; $P = 0.02$; $n = 15$). Dispersing bears moved primarily to the northeast and southwest following the predominant ridgelines of the Appalachian Mountains through western Virginia (Figure 5).

Resident yearling males left their mothers' home ranges during June ($n = 1$), July ($n = 2$), August ($n = 2$), and September ($n = 2$). Two resident yearling males remained in their mother's home range. We were unable to determine the month that 2 resident

Table 14. Distance traveled between initial and final locations^a of radio-marked subadult American black bears on the George Washington - Jefferson National Forests, Virginia, 1999-2002.

Group	Age / Sex	n	Mean (km)	Median (km)	SE	Range (km)
Resident ^b	1-year-old males	11	15.7	5.2	6.2	1.8 – 63.6
Summer ^c	1-year-old males	21	14.7	6.5	4.1	0.9 – 80.0
Resident	2-year-old males	0	-	-	-	-
Summer	2-year-old males	19	12.2	5.9	3.2	1.9 – 61.4
Resident	3-year-old males	0	-	-	-	-
Summer	3-year-old males	6	11.6	9.0	3.2	2.5 – 23.9
Resident	1-year-old females	13	2.2	1.6	0.5	0.3 – 5.7
Summer	1-year-old females	5	6.9	6.0	2.3	1.7 – 13.9
Resident	2-year-old females	11	3.2	1.7	1.0	0.3 – 11.4
Summer	2-year-old females	14	1.8	1.7	0.3	0.2 – 4.2
Resident	3-year-old females	4	1.0	0.9	0.4	0.3 – 2.0
Summer	3-year-old females	14	2.3	1.7	0.5	0.3 – 7.1

^a Initial locations: yearling den for residents or capture site for summer captures
 Final locations: drop site of transmitter, harvest site, or 2002 den site

^b Born on study area

^c Birth location unknown

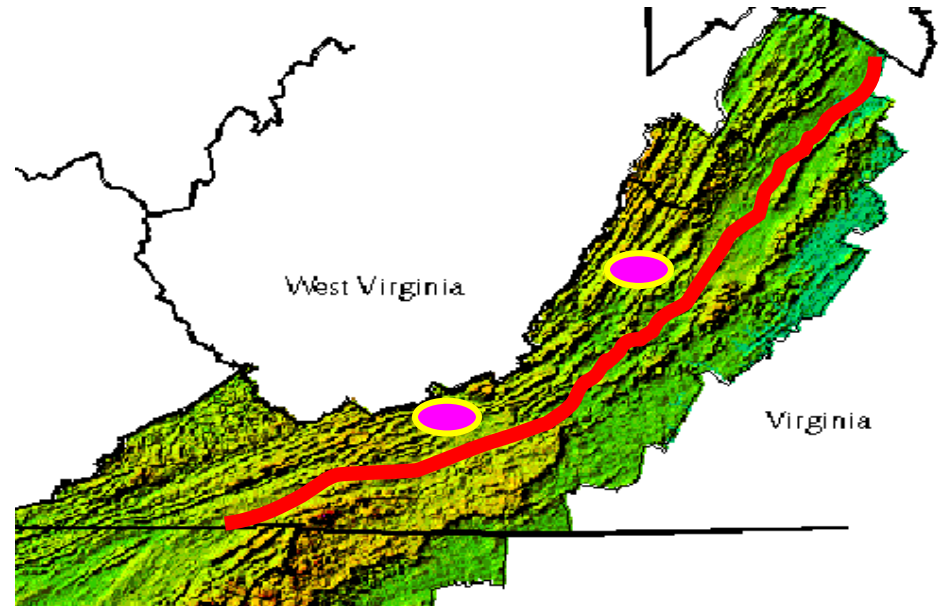
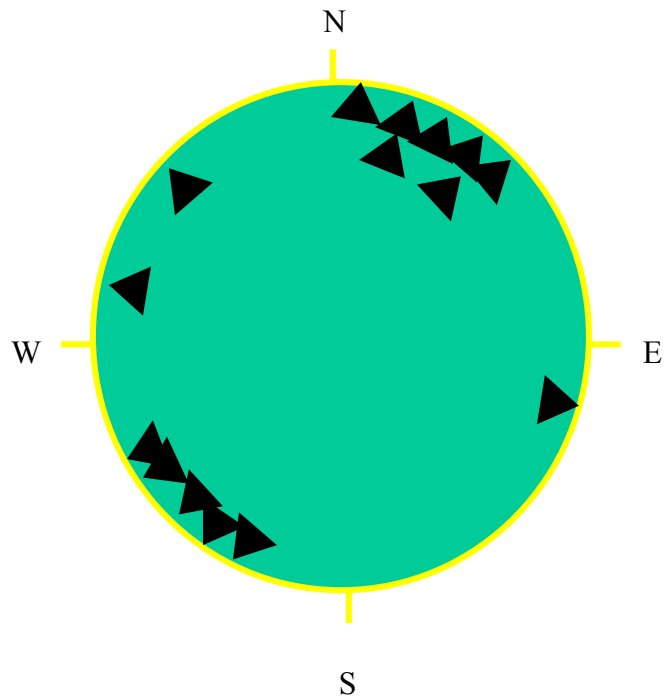


Figure 5. Direction of travel for all subadult males moving > 15 km in the George Washington - Jefferson National Forests, Virginia, 1999-2002. Study sites are represented with ovals and Interstate 81 with the bold line to the east of the study sites. Most subadult bears dispersed along the direction of predominant ridgelines.

yearling males left, but 1 left between July and October as a yearling and a second male left between July as a yearling and December as a 2-year-old (i.e. over 18 month period).

The logistic regression analysis indicated that neither males ($\chi^2 = 2.07$, $P = 0.15$ $df = 1$) nor females ($\chi^2 = 0.0002$, $P = 0.99$, $df = 1$) increased their risks of mortality with increased distance traveled. This conclusion was reinforced by chi-square analyses indicating that neither resident males ($\chi^2 = 0.09$, $P = 0.77$, $df = 2$) nor summer captured males ($\chi^2 = 1.62$, $P = 0.20$, $df = 2$) increased their risk of mortality with increased distance moved (Table 15).

DISCUSSION

We decided on a more stringent definition of dispersal, building on the definitions of Alt (1978) and Rogers (1987). We reasoned that a minimum dispersal distance of 20 km for male bears and 8 km for female bears would likely keep subadult bears from overlapping with their mother's home range as they established their own adult home ranges. Bears that disperse this distance, particularly males, presumably would receive some of the advantages dispersal confers, such as reduction of feeding competition with female kin, reduced mate competition with male kin, and inbreeding avoidance (Rogers 1987).

Subadult female black bears generally establish a home range within or adjacent to their mother's home range, although occasional female dispersal has been reported (Rogers 1987; Schwartz and Franzmann 1992). In Pennsylvania, all of 7 subadult female black bears remained primarily within their mother's home range without dispersing, and 91% of the distances between trapping and kill sites for subadult females were less than 10 km. (Alt 1978). In Minnesota, 3 of 31 subadult females dispersed 3, 8, and 11 km

Table 15. Fates of subadult American black bears by distance traveled between initial and final locations^a in the George Washington – Jefferson National Forests, Virginia, 1999-2002.

Group / Fate	Distance traveled (km)											
	0-5		5-10		10+							
Residents ^b	M (5) ^c		F (16)		M (2)		F (4)		M (4)		F (0)	
Alive	1	9	1	2	0	0	0	0	0	0	0	0
Unknown	2	5	0	2	2	2	0	2	0	2	0	0
Dead	2	2	1	0	2	0	2	0	2	0	0	0
Summer Captures ^d	M (14)		F (23)		M (15)		F (3)		M (15)		F (0)	
Alive	7	13	5	2	3	0	3	0	3	0	0	0
Unknown	1	7	2	1	2	0	1	0	2	0	0	0
Dead	6	3	8	0	10	0	10	0	10	0	0	0

^a Initial locations: yearling den for residents or capture site for summer captures
Final locations: drop site of transmitter, harvest site, or 2002 den site

^b Born on study area

^c Number of subadult bears for each sex and distance category

^d Birth location unknown

(Rogers 1987). In Massachusetts, 1 of 13 females moved from her mother's home range (Elowe and Dodge 1989). In Alaska, only 1 of 30 subadult females dispersed, and it died the year of dispersal. White et al. (2000) reported that no female black bears dispersed from a Louisiana study area. During this study, none of 20 resident subadult females dispersed from their mother's home range, and none of 26 summer capture subadult females moved > 8 km between initial and final locations on our study sites. The complete lack of female dispersal on our study site may be associated with our low levels of female harvest and high density (Klenzendorf 2002), which may create fewer open home range spaces. Lack of dispersal among female subadult black bears across North America suggests that females gain advantages such as securing a home range and resources by staying in their natal areas (Rogers 1987), and should increase survival and reproductive potential.

Current knowledge suggests that male bears disperse from their natal areas in their first or second year to seek and establish a home range of their own (Rogers 1987, Schwartz and Franzmann 1992). Long distance movements (e.g. >60 km) by our yearling and 2-year-old age classes indicate that dispersal occurs for this age group in western Virginia. By age 3, males may no longer be dispersing since the greatest distance traveled by a 3-year-old was 23.9 km, which is similar to the greatest adult male movement (21.8 km) on our study areas. Nine of 11 resident subadult males left their mother's home range, but by our definition of dispersal, only 3 of the 11 dispersed. It is possible that some resident subadults continued dispersal movements as 2-year-olds, but they did not retain their radio transmitters long enough to test this hypothesis. We did recapture 1 resident male as a 2-year-old approximately 8 km outside his mother's home

range. He remained there during the summer and was photographed by remote cameras in October. It is unclear whether he had established a permanent range.

There may be several reasons why most resident males (8 of 11) did not, by our definition, disperse. First, we had poor success keeping transmitters on resident yearling males for > 1 year. Data for summer captures revealed that 2-year-old bears made long distance movements and may not have completed their dispersal movements. Thus resident males, marked by us as yearlings, may have dispersed after losing their transmitters. Second, our definition of dispersal may be too stringent. Movement from the mother's home range that is < 20 or 8 km for subadult males and females, respectively, may still confer some advantages from dispersal and not come with the potentially high cost (i.e. physiological and survival) of movement over longer distances. Third, although the literature indicates that male bears are likely to disperse, all males may not disperse due to genetic variation among individuals who may have a greater/lesser propensity to move long distances. Fourth, some males may have found suitable habitat, close to their natal home range, left vacant by a harvested or otherwise deceased adult male bear. Finally, it is not clear what role density and habitat play in encouraging or stifling dispersal movements in subadult black bears. Lindsay and Meslow (1977) reported delayed dispersal associated with a high- density black bear population on Long Island, Washington.

Our results were similar to those in Pennsylvania where 6 of 7 subadult males left their mother's home range; 4 dispersed as yearlings and 2 dispersed sometime between age 1 and 3. Eleven of 15 (14M : 1F) subadult bears were suspected to have dispersed as yearlings, 3 as 2 year olds, and 1 as a 3 year old (Alt 1978). In Florida, 4 radio collared

subadult males dispersed, 2 as yearlings and 2 as 2-year-olds (Wooding and Harding 1994). Schwartz and Franzmann (1992) reported that 18 of 21 male black bears born in their study areas in Alaska dispersed. Six of the 18 males that dispersed left as yearlings, 10 as 2 year olds, and 2 as 3 year olds. Rogers (1987), in Minnesota, reported that all males born on his study area dispersed. Among 20 dispersal observations, no yearlings dispersed, but 13, 5, and 2 dispersed as 2, 3, and 4 year olds, respectively. Reynolds and Beecham (1980) in Idaho reported that 9 of 10 (7F : 3M) yearlings remained in their mother's home range and did not disperse as yearlings. One male dispersed 20 km away as a yearling.

Reports in the literature of dispersal by black bears suggests that bears in eastern North America may disperse at an earlier age than bears in other parts of North America. Alt (1978) speculated that early maturation and heavier weights (> 91 kg) of yearling bears in Pennsylvania was responsible for their dispersal. Summer capture weights of yearling males in our study area ($x = 40.6$; range = 18.2 – 79.5; $n = 105$) are comparable to 2-year-old males in Minnesota (range = 29 – 59 kg; $n = 17$) where dispersal did not occur in the yearling age class (Rogers 1987). Similarly, Alaskan black bears tended to disperse as 2-year-olds, although weights were not given (Schwartz and Franzmann 1992). Summer weight of the subadult males on our study area was not correlated with dispersal behavior. Reasons for differing ages of dispersal for subadult males are unclear.

Dispersal in subadult males appears to be voluntary and likely confers advantages to dispersing bears (Rogers 1987). Resident subadult males in this study tended to leave their mother's home range by the end of summer, but made long distance movements in

all months up to denning. Dispersing individuals often moved during months (i.e. October – December) when testosterone levels are low in adult males (Garshelis and Hellgren 1994), and when some adult males were already denned (i.e. early winter), thus aggressive interactions may have played little role in dispersal. Food shortages did not appear to motivate dispersal as no hard or soft mast failures occurred during this study.

Although we reported that only 3 of 11 resident male subadults dispersed >20km, it is likely that some of the other's dispersed > 20 km after they dropped their radio-transmitters. We speculate that adult females initially separate themselves from their yearling offspring for an opportunity to breed. The adult female tolerates encounters with female offspring, but may continue to be aggressive toward male offspring. Male yearlings are gradually forced off their natal areas, or leave them willingly. Yearling and subadult males likely encounter adult males who push the younger bears out of their breeding areas or home ranges. It may take yearling and subadult males more than a year to find an unoccupied home range, especially in high density populations. Subadults that fail to establish home ranges likely are forced into sub optimal or non-habitat where survival is low. In a hunted population a subadult male's best chance may be to occupy the home range of a harvested adult male.

Black bears can cover substantial distances during dispersal. Our distance movements are similar to dispersal distances and movements reported for subadult males in other eastern states. We documented that subadult males dispersed up to 80 km, and 20% of our subadult males moved >20 km. Clevenger and Pelton (1990) reported a movement of 66 km before returning to the mother's home range to den. In Florida, 4 subadult males dispersed 22, 35, 56, and 56 km (Wooding and Hardisky 1994). In

Pennsylvania, greatest dispersal distance by a subadult male was 53 km (5-53 km; Alt 1978). In Massachusetts, Elowe and Dodge (1989) reported that 8 subadult males moved between 30 - 200km, but did specify an average dispersal distance. In Minnesota, Rogers (1987) reported average dispersal distances of 61 km (13 –219 km) and 75 km (20-224 km) for 18 subadult males born in his Minnesota study area and 19 subadult males that wandered through the study site, respectively. Although subadult males are capable of moving greater distances (Rogers 1987, Elowe and Dodge 1989), an upper boundary of approximately 100 km may be usual for most eastern states, particularly in the southern Appalachian Mountains.

Wandering, which occurs when a subadult leaves its mother's range for some period of time and returns (Schwartz and Franzmann 1992), was noted for subadult females and males during this study. One resident subadult female was captured as a 2-year-old approximately 8 km from her mother's home range, but she returned and was consistently located inside her mother's home range until her harvest. Another resident female traveled outside her mother's home range to approximately 11.4 km before returning. A summer captured subadult female moved 13.9 km from her capture location as a yearling, but was located within 5 km of her capture location as a 2-year-old. Two resident yearling males wandered 4 km and 23 km outside their mother's home ranges before returning in September and August, respectively. Schwartz and Franzmann (1992) noted 7 yearling males wandered from their mother's home ranges and returned to their mother's home range to den prior to dispersing. Clevenger and Pelton (1990) reported that 3 of 6 yearlings made long distance exploratory trips during the fall that culminated in a return to or near the mother's home range to den by winter. Separating

dispersal movements from more localized movements when a bear has traveled only a short distance is very difficult, especially for subadult females.

Dispersing bears did not disperse randomly. The Appalachian Mountains run in a southwest to northeast direction through western Virginia, and predominant ridgelines appeared to be used as dispersal corridors for subadult males in western Virginia. A lack of eastward or southeastward dispersal may indicate a hesitancy to leave the national forest lands and travel over more agriculturally developed lands. The 1 subadult male that dispersed eastward stopped after moving approximately 34 km by mid July and remained on National Forest land. He remained in the area until his harvest in December. The heavily populated Shenandoah Valley (approximately 318,000; Weldon Cooper Center for Public Service, University of Virginia, unpublished data) and Interstate 81 lies to the east of the George Washington – Jefferson National Forests and may be a barrier to eastward and southeastward dispersal.

All mortality to subadult bears during this study was due to harvest, and it appears that dispersal may have a cost in survival. The percentage of bears harvested was greatest for subadult males who moved > 10 km ($n = 12$ of 19; 63%) than subadult males who moved < 10 km ($n = 17$ of 36; 47%). Eight of 11 (73 %) subadult males that moved > 20 km (i.e. dispersed) were harvested while all 4 bears (100%) that dispersed > 40 km were harvested. Logistic regression revealed that mortality (i.e. harvest) did not increase with increasing distance moved for radio-marked bears by sex. However, male bears who moved the greatest distances were often harvested, and we may have been unable to find a relationship due to lower than needed male sample size. Our results were similar to those in Alaska where 14 of 18 dispersing subadult males died, contact was lost with 2,

and 2 were still alive by the study's end. Nine of the 14 bears that died, died during the same year as dispersal. Non-dispersing females (n=29) survived longer than males. Subadult males were 2–3 times less likely to survive to adulthood than subadult females (Schwartz and Franzmann 1992). During this study 29 of 55 (53 %) subadult males with radio transmitters were harvested, while 5 of 46 (11 %) females outfitted with transmitters were harvested. Subadult males were almost 5x less likely to reach adulthood than subadult females on our study areas.

MANAGEMENT RECOMENDATIONS

Female range expansion is slow so managers should monitor sex ratio of harvest to insure females are not over-harvested. As subadult females did not disperse, an over-harvest of females in an area can make recruitment back into the area unlikely and could be a cause of concern. However, it is unclear how bear population density affects movement of adult females into vacant and new areas. Barriers to movement such as developed lands and major traffic corridors may require translocation of female bears to reach and establish populations in new areas.

Researchers have recognized the need for corridors to connect isolated populations of black bears (Clark and Pelton 1998, Miller et al. 1998). Parameters needed for effective corridor use by black bears have yet to be determined (Hellgren and Vaughan 1994), but forested tracts of land are most frequently sought as connectors. Hellgren and Vaughan (1994) noted that rivers draining the Great Dismal Swamp in eastern Virginia may serve as natural corridors to existing bear habitat along the Atlantic coast. In mountain populations, biologists may enhance connectivity among bear

populations if corridors are established in the direction of predominant ridgelines or other landscape level features, which may aid or direct dispersing subadult bears.

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APPENDICES

Appendix 1. Survival estimates for male and female 1-, 2-, and 3-year-old black bears calculated from the Cormack-Jolly-Seber model, the dead recoveries model, and Burnham's combined model and used in Chi-squared tests for further pooling of age classes.

Age/Sex class	CJS		Model Dead recoveries		Burnham's combined	
	Estimate	95% C.I.	Estimate	95% C.I.	Estimate	95% C.I.
1-year-old female	0.69	0.33 - 0.91	0.75	0.48 - 0.91	0.80	0.58 - 0.93
2-year-old female	0.72	0.44 - 0.90	0.80	0.61 - 0.91	0.85	0.72 - 0.93
3-year-old female	0.92	0.06 - 1.00	0.90	0.72 - 0.97	0.93	0.79 - 0.98
1-year-old male	0.24	0.13 - 0.42	0.18	0.07 - 0.39	0.33	0.21 - 0.49
2-year-old male	0.45	0.29 - 0.62	0.39	0.22 - 0.59	0.55	0.42 - 0.68
3-year-old male	0.53	0.28 - 0.77	0.57	0.32 - 0.79	0.72	0.55 - 0.84

VITA

Daniel James Lee was born to Jim and Debbie Lee in Birmingham, Alabama on January 22, 1975. He was raised in Mt. Olive, Alabama and attended Gardendale High School. In 1999, he graduated with a B. S. degree in Wildlife Science from Auburn University. While at Auburn, he worked as a technician for a food preference of mourning dove study under Dr. Ralph Mirarchi and a mark-recapture study of gopher tortoises in Conecuh National Forest under Dr. Craig Guyer. He married Stephanie Loggins of Pinson, Alabama in June 1999. Following graduation, he enrolled to Virginia Polytechnic Institute & State University in the Department of Fisheries and Wildlife Sciences as a graduate student on the Cooperative Alleghany Bear Study. He studied survival, family breakups, and dispersal of yearling and subadult black bears in western Virginia. He assisted on a study of desert bighorn sheep in the Grand Canyon National Park, Arizona in April 2002. He was contracted by the Conservation Management Institute to conduct breeding bird surveys for Eastern Virginia National Wildlife Refuge, to assist with a western Virginia grassland bird study, and to survey birds for a bird atlas for Fort Chaffee Maneuver Training Center, Arkansas. He became an Associate Wildlife Biologist with The Wildlife Society in October 2002.