

Dispersal movements by subadult American black bears in Virginia

Daniel J. Lee^{1,3} and Michael R. Vaughan^{2,4}

¹Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University,
106 Cheatham Hall, Blacksburg, VA 24061, USA

²U.S. Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University,
148 Cheatham Hall, Blacksburg, VA 24061, USA

Abstract: Dispersal plays an important role in the population dynamics of large carnivores; however, dispersal by subadult American black bears (*Ursus americanus*) is poorly understood in Virginia, as well as in North America. Thus, during 1999–2002, we studied the movements of 31 (11M:20F) subadult black bears born on 2 study areas in western Virginia and 70 (44M:26F) subadult bears captured during the summer on the study areas. No radiomarked, natal-captured, subadult female bears exhibited dispersal behavior while 3 of 11 (27%) radiomarked, natal-captured, subadult males dispersed. Natal-captured and summer-captured male bears moved greater distances than females from yearling den location and summer-capture locations. The longest subadult male movement was 80 km (\bar{x} = 13.4 km, range = 0.6–80.0 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; bears appeared to follow the orientation of the predominant ridgelines and avoided leaving the national forest. All known mortality of dispersing and non-dispersing bears was due to harvest. Lack of female dispersal may require managers to control local harvest of females to provide for continued reproduction and growth in some areas.

Key words: American black bear, dispersal, movement, radio-telemetry, subadults, *Ursus americanus*, Virginia, yearlings

Ursus 14(2):162–170 (2003)

Dispersal is one of the least studied demographic parameters in North American black bear populations (Rogers 1977, Clevenger and Pelton 1990, Schwartz and Franzmann 1992). Dispersal in black bears generally occurs in the subadult age class and primarily by males (Rogers 1987a, Schwartz and Franzmann 1992). Subadult bears are capable of traveling long distances (Rogers 1987b), which has implications for genetic variability among bear populations, usefulness of bear refuges, and consequences for survival (Clevenger and Pelton 1990). However, many researchers studying black bears are reluctant to radiocollar fast growing subadult animals because of the potential for neck injuries 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 establish-

ing and maintaining black bear populations (Alt 1978). Immigration of subadult male bears was 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). Determining dispersal patterns may be helpful or even 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 of movements varied between sexes, determine the time of

³dalee6@vt.edu ⁴mvaughan@vt.edu

year dispersal occurs, determine if bears dispersed in a random direction, and examine the relationship between dispersal distance and survival.

Study areas

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

The 1,540 km² southern study site 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 (U.S. Department of Agriculture Soil Conservation Service 1965). Elevation ranges from 492 m along the Craig Creek drainage to 1,378 m at Mountain Lake.

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. Mean yearly precipitation is 86 cm and occurs mostly between April and September. Mean snowfall is 71 cm/year. The mountains of the study area usually receive more precipitation and average 2.8–5.6°C cooler than the Shenandoah Valley (Rawinski et al. 1994).

Vegetation on the 2 study sites is similar. Forest cover types on the study areas include: eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*)–beech (*Fagus grandifolia*)–yellow birch (*Betula alleghaniensis*), chestnut oak (*Quercus prinus*), pitch pine (*Pinus rigida*), white oak (*Q. alba*)–black oak (*Q. velutina*)–northern red oak (*Q. rubra*), yellow poplar (*Liriodendron tulipifera*)–white oak–northern red oak–eastern white pine (*P. strobus*), northern red oak, and barren and brush cover such as mountain laurel (*Kalmia latifolia*) or scrub oak (*Q. ilicifolia*) (Rawinski et al. 1994).

Methods

Fieldwork was conducted from June 1999 to April 2002. We trapped bears during June to August each year with spring-activated Aldrich foot snares and culvert traps, and we entered the dens of radiocollared bears during January to March each year. We used a 2:1 mix-

ture of ketamine hydrochloride (Ketaset, Fort Dodge Animal Health, Fort Dodge, Iowa, USA) and xylazine hydrochloride (Rompun, Bayer Corporation, Shawnee Mission, Kansas, USA; concentration of 300 mg/ml) at a dosage rate of 1 cc/45.4 kg (100 pounds estimated) of body weight to immobilize bears. Drugs were administered with a Capchur gun (Palmer Chemical Company, Douglasville, Georgia, USA) 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, Colorado, USA; concentration of 5 mg/ml) was administered at a dosage of 2 cc/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 roughly monthly and gave priority to bears not found during the ground surveys. Ground telemetry (Telonics, Mesa, Arizona, USA) was conducted along forest roads and trails. We walked to 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 in their second year of life as yearlings, 2- and 3- year olds as subadults, and ≥4-year olds as adults. We separated radiomarked subadults into 2 groups: natal-captured bears, which were known to be born on the study site to a known adult female, and summer-captured bears, for which location of birth was unknown. Distance moved for each subadult was calculated as a straight line between initial and final locations, which was not always the maximum distance that a subadult bear moved during the study. Initial locations were the yearling den sites (where bears emerged from den as a yearling) for natal-captured bears and capture sites for summer-captured bears. Final locations for both groups were transmitter drop sites, harvest sites, or 2002 den sites if the bear wore its transmitter until the end of the study.

We considered dispersal for a male bear to have occurred if he moved from the center of his mother's home range to an area where he would no longer overlap her home range when developing his adult male home range. In our case this required a movement >18 km between initial and final locations for subadult males, which we determined by adding the radius of an average

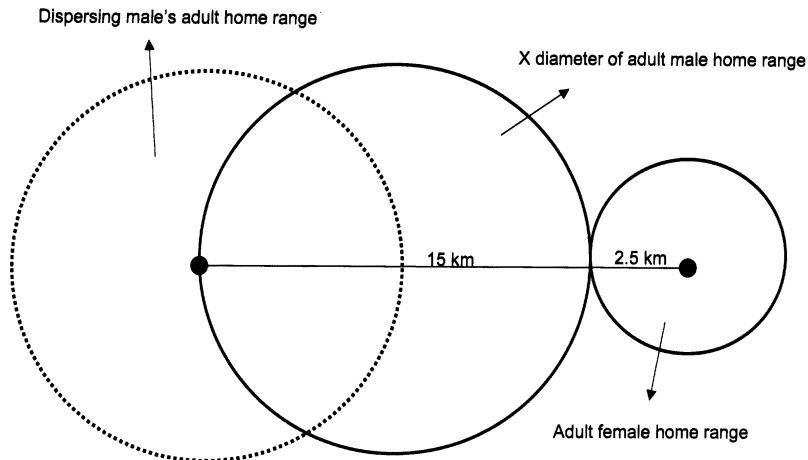


Fig. 1. Dispersal movement by a subadult male black bear. A male dispersed from his mother's home range if he moved a distance equal to the mean diameter of an adult male home range. This distance ensured that the dispersing male would not associate with his mother or with female siblings remaining near the mother's home range.

adult female's home range ($\bar{x} = 2.5$ km) to the average diameter of an adult male home range ($\bar{x} = 15$ km) for our study site (Fig. 1). We added a diameter, rather than a radius, so that the home range established by the dispersing individual would not overlap its mother's home range if it moved substantially (movement equal to an adult male's home range diameter) toward its mother's home range.

We constructed 95% fixed kernel home ranges in ArcView 3.2 (Environmental Systems Research Institute, Inc., Redlands, California, USA) for resident adult females and their female offspring. Subadult females whose home ranges overlapped 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 determined by summing the mean radius ($\bar{x} = 2.5$ km) and mean diameter ($\bar{x} = 5$ km) of adult female home ranges in our study area. This represented the minimum distance that a subadult female needed to travel from the center of her mother's home range to develop a home range that did not overlap her mother's home range.

We used Fisher's exact test to compare behavioral (dispersal vs. non-dispersal) differences between sexes for natal-captured 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 natal- and summer-captured bears, and for each

sex between groups. We quantified relationships between summer weight and distance traveled for yearling and 2-year-old males using Pearson's correlation coefficient. We used Rayleigh's test (Batschelet 1981) to test the hypothesis that direction of movement was random for natal-captured bears, summer-captured bears, all males moving >20 km, and all males moving >15 km. We used logistic regression to fit relationships between probability of mortality for radio-marked male and female subadult bears and distance traveled. All tests were conducted in SAS (SAS Institute, Inc., Cary, North Carolina, USA), and we used $\alpha = 0.05$ as our significance level.

Results

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

None of 20 natal-captured females exhibited dispersal behavior, whereas 9 of 11 (82 %) natal-captured males left their mother's home range. Three of 11 (27%) natal-captured males dispersed >20 km ($P = 0.04$). Home ranges for 13 of 20 (65%) natal-captured females overlapped their mother's home range. None of the remaining 7 natal-captured females (mother's home range unknown) moved >8 km from their yearling den site to their final location (dispersal behavior); thus, no subadult female met our definition of dispersal. One natal-captured and 1 summer-captured female moved >8 km to den, but both returned to their previous home ranges (which overlapped with their mother's home range and were <8 km from capture site) after den emergence and were not considered to have dispersed.

Natal-captured ($\chi^2 = 8.54$; 2 df, $P = 0.01$) and summer-captured ($\chi^2 = 22.02$; 2 df, $P < 0.01$) subadult males moved farther, respectively, than subadult females

Table 1. Length of time (days) that radiomarked subadult black bears wore ear-tag transmitters or radiocollars on the George Washington–Jefferson National Forests, Virginia, 1999–2002.

| Sex | Fate | <i>n</i> | Mean (days) | Median (days) | Range (days) |
|--------|---------|----------|-------------|---------------|--------------|
| Female | alive | 26 | 331 | 188 | 68–1,179 |
| | unknown | 15 | 268 | 256 | 90–535 |
| | dead | 5 | 448 | 539 | 98–636 |
| Male | alive | 17 | 311 | 283 | 24–907 |
| | unknown | 9 | 231 | 213 | 91–331 |
| | dead | 29 | 174 | 170 | 46–512 |

for all distance categories. No natal- or summer-captured subadult female moved >10 km between initial and final locations, whereas 36% of natal-captured and 34% of summer-captured males moved >10 km between initial and final locations. We did not detect a difference between natal- and summer-captured subadult males in distance traveled between initial and final locations ($\chi^2 = 1.21$, 2 df, $P = 0.547$); the same was true for subadult females ($\chi^2 = 0.63$, 2 df, $P = 0.428$). Natal- and summer-captured yearlings and 2-year-old summer-captured male bears had higher mean distances ($\bar{x} = 15.7$, 14.7, and 12.2 km, respectively) and moved greater distances (>60 km) than 3-year-old males ($\bar{x} = 11.6$ km, longest = 23.9 km; Table 2). Weight during summer handling was not correlated with distance traveled by yearling ($r = -0.198$, $P = 0.30$, $n = 29$) or 2-year-old ($r = 0.044$, $P = 0.87$, $n = 17$) males.

Direction of travel for dispersing male bears did not differ from random for all natal-captured males ($r = 0.094$, $P = 0.90$) or all summer-captured males ($r = 0.184$, $P = 0.24$). However, direction of travel differed from random for males that moved >20 km ($r = 0.596$;

$P = 0.02$; $n = 11$) and males that moved >15 km ($r = 0.513$; $P = 0.02$; $n = 15$). Dispersing bears moved primarily to the northeast and southwest following the predominant ridgelines of the Appalachian Mountains through western Virginia (Fig. 2).

Natal-captured yearling males left their mothers' home ranges during June ($n = 1$), July ($n = 2$), August ($n = 2$), and September ($n = 2$), and 2 remained in their mother's home range. We were unable to determine the month that 2 natal yearling males left, but 1 left between July and October as a yearling and a second left between July of his yearling year and December the following year (as a 2-year-old).

Logistic regression indicated that neither males ($\chi^2 = 2.07$, 1 df, $P = 0.15$) nor females ($\chi^2 = 0.0002$, 1 df, $P = 0.99$) increased their risk of mortality with increased distance traveled (Table 3). Of subadult males who moved >10 km and <10 km, 63% (12 of 19) and 47% (17 of 36), respectively, were harvested. Eight of 11 (73%) subadult males that moved >20 km (dispersed) were harvested, and all 4 bears (100%) that dispersed >40 km were harvested.

Table 2. Distance traveled between initial and final locations^a of radiomarked subadult American black bears on the George Washington–Jefferson National Forests, Virginia, 1999–2002.

| Group | Cohort | <i>n</i> | Mean (km) | Median (km) | SE | Range (km) |
|---------------------|--------------------|----------|-----------|-------------|-----|------------|
| Natal ^b | yearling males | 11 | 15.7 | 5.2 | 6.2 | 1.8–63.6 |
| Summer ^c | yearling males | 21 | 14.7 | 6.5 | 4.1 | 0.9–80.0 |
| Natal | 2-year-old males | 0 | — | — | — | — |
| Summer | 2-year-old males | 19 | 12.2 | 5.9 | 3.2 | 1.9–61.4 |
| Natal | 3-year-old males | 0 | — | — | — | — |
| Summer | 3-year-old males | 6 | 11.6 | 9.0 | 3.2 | 2.5–23.9 |
| Natal | yearling females | 13 | 2.2 | 1.6 | 0.5 | 0.3–5.7 |
| Summer | yearling females | 5 | 6.9 | 6.0 | 2.3 | 1.7–13.9 |
| Natal | 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 |
| Natal | 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 |

^aInitial locations: yearling den for natal–capture and capture site for summer–capture; final locations: drop site of transmitter, harvest site, or 2002 den site.

^bBorn on study area.

^cBirth location unknown.

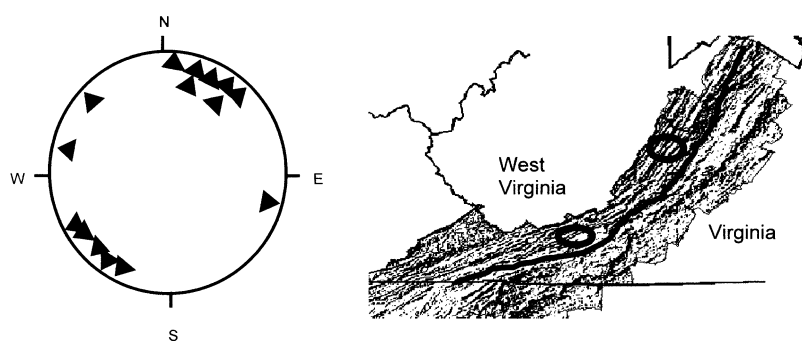


Fig. 2. Direction of travel for all subadult males moving >15 km in the George Washington–Jefferson National Forests, Virginia, 1999–2002. Study sites are represented with ovals; bold line east of the study sites represents Interstate Highway 81. Most subadult bears dispersed along the direction of predominant ridgelines.

Discussion

We developed a definition of dispersal building on the definitions of Alt (1978) and Rogers (1987b). We reasoned that a minimum dispersal distance of 18 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 adult home ranges. Bears that disperse this distance, particularly males, presumably receive some advantages dispersal confers, such as reduction of feeding competition with female kin, reduced mate competition with male kin, and inbreeding avoidance (Rogers 1987a).

Subadult female black bears generally establish a home range within or adjacent to their mother's home range, although female dispersal has been reported (Rogers 1987b, Schwartz and Franzmann 1992). In Pennsylvania, all of 7 subadult female black bears remained primarily within their mother's home range, and 91% of the distances between trapping and kill sites for subadult females were <10 km. (Alt 1978). In Minnesota, 3 of 31 subadult females dispersed 3, 8, and 11 km (Rogers 1987b). In Alaska, only 1 of 30 subadult females dispersed, and it died the year of dispersal (Schwartz and Franzmann 1992). White et al. (2000) reported that no female black bears dispersed from a Louisiana study area. During the present study, none of 20 natal-captured females dispersed from their mother's home range, and none of 26 summer-captured 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 low levels of female harvest and high bear density (Klenzendorf 2002), which may create fewer open

spaces for subadult females to be independent of their mother. 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 1987a).

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 1987b, Schwartz and Franzmann 1992). Movements >60 km by bears in 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, because 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 natal-captured 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 natal-captured subadults continued dispersal movements as 2-year olds, but they did not retain their radio transmitters long enough to test this hypothesis. We recaptured 1 natal-captured 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 established his adult home range. Another subadult male moved 23 km from his natal-captured site but returned and was killed by a hunter. He was not considered to have dispersed.

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-captured bears revealed that 2-year-old bears made long distance movements, and natal-captured males, marked by us as yearlings, may have dispersed after losing their transmitters. Thus, we urge caution when interpreting our estimates of dispersal movements because we were unable to follow any subadult male bears until they established home ranges as adults. 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 (physiological and survival costs)

Table 3. 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 | |
| Natal-capture ^b | M (5) ^c | F (16) | M (2) | F (4) | M (4) | F (0) |
| alive | 1 | 9 | 1 | 2 | 0 | 0 |
| unknown | 2 | 5 | 0 | 2 | 2 | 0 |
| dead | 2 | 2 | 1 | 0 | 2 | 0 |
| Summer-capture ^d | M (14) | F (23) | M (15) | F (3) | M (15) | F (0) |
| alive | 7 | 13 | 5 | 2 | 3 | 0 |
| unknown | 1 | 7 | 2 | 1 | 2 | 0 |
| dead | 6 | 3 | 8 | 0 | 10 | 0 |

^aInitial locations: yearling den for natal-capture and capture site for summer-capture; final locations: drop site of transmitter, harvest site, or 2002 den site.

^bBorn on study area.

^cNumber of subadult bears for each sex and distance category.

^dBirth location unknown.

of movement over longer distances. Third, although the literature indicates that male bears are likely to disperse (Rogers 1987a), not all males may disperse due to genetic variation—some individuals may have a lesser propensity to move long distances. Fourth, some males may have found suitable habitat close to their natal home range left vacant by the death of an adult male bear. Finally, it is not clear what role density and habitat play in encouraging or stifling dispersal in subadult black bears. Lindzey 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 between ages 1 and 3. Eleven of 15 subadult male and female 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 radiocollared 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 (1987b) found that dispersal occurred for all males born on his study area in Minnesota. Among 20 dispersal observations, no yearlings were observed to disperse, 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 as a yearling.

North American data on age of dispersal suggests that dispersal may occur at an earlier age (as 1-year olds) for black bears in eastern populations than those in western populations. Alt (1978) speculated that early maturation and heavier weights (>91 kg) of yearling bears in Pennsylvania was responsible for their dispersal. However, summer-captured weights of yearling males in our study area (\bar{x} = 40.6; range = 18.2–79.5; n = 105) were comparable to yearling weights in Minnesota (range 29–59 kg; n = 17), where dispersal did not occur in the yearling age class (Rogers 1987b). Similarly, Alaskan black bears tended to disperse as 2-year olds, although weights were not given (Schwartz and Franzmann 1992). Summer weights of the subadult males on our study area were 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 them (Rogers 1987a). Natal-captured males tended to leave their mother's home range by the end of summer, but yearling and subadult males moved long distances in all months up to denning. Dispersing individuals often moved during months when testosterone levels are low in adult males (Oct–Dec; Garshelis and Hellgren 1994) and when some adult males were already denning (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.

Black bears can cover substantial distances during dispersal. Our distance movements are similar to dispersal distances and movements previously reported for subadult males in the eastern USA. 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 the bear returned 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 30–200 km, but they did not specify an average dispersal distance. In Minnesota, Rogers (1987b) 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 1987b, Elowe and Dodge 1989), an upper boundary of approximately 80 km may be usual for most eastern states, particularly in the southern Appalachian Mountains.

Exploratory excursions, which occur when a subadult leaves its mother's range for some period and returns (Schwartz and Franzmann 1992), were noted for subadult females and males during this study. One natal-captured 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 natal-captured female traveled approximately 11.4 km outside her mother's home range before returning. A summer-captured subadult female moved 13.9 km from her capture location as a yearling to den, but was regularly located within 5 km of her capture location as a 2-year old. Two natal-captured yearling males moved 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 moved from their mother's home ranges but returned to den prior to dispersing. Clevenger and Pelton (1990) reported that 3 of 6 yearlings made long distance explorations during the fall then returned 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 in random directions. The Appalachian Mountains run southwest to northeast through western Virginia (Fig. 2), 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 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 being killed by a hunter in December. The heavily populated Shenandoah Valley (approximately 318,000 people; Weldon Cooper Center for Public Service, University of Virginia, Charlottesville, Virginia, USA, unpublished data) and Interstate Highway 81 lie to the east of the George Washington–Jefferson National Forests and may be a barrier to eastward and southeastward dispersal.

All recorded mortality to subadult bears during this study was due to hunter harvest. Logistic regression revealed that harvest did not increase with increasing distance moved for radiomarked bears by sex. However, male bears that moved the greatest distances (all bears that moved >40 km) were often harvested, and we may have been unable to find a relationship due to insufficient 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 (Schwartz and Franzmann 1992). Nine of the 14 bears that died during the Alaska study died the year of dispersal. Non-dispersing females ($n = 29$) survived longer than males. Subadult males were 2 to 3 times less likely to survive to adulthood than subadult females (Schwartz and Franzmann 1992). During our study, 29 of 55 (53%) subadult males with radio transmitters were harvested, whereas 5 of 46 (11%) females outfitted with transmitters were harvested. Subadult males were almost 5 times less likely to reach adulthood than subadult females on our study areas.

Management recommendations

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

Some 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, connectivity may be enhanced 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.

Acknowledgments

Financial support for this project came from Virginia Polytechnic Institute and State University, the Virginia Department of Game and Inland Fisheries, U.S. Department of Agriculture Forest Service, U.S. Geological Survey—Biological Research Division, and the Virginia Bear Hunter's Association. Thanks to the many technicians and volunteers who captured and tracked dispersing black bears during the project. This manuscript was greatly improved by the comments of R. Harris, J. Linnell, and 2 anonymous reviewers.

Literature cited

- ALT, G.L. 1978. Dispersal patterns of black bears in north-eastern Pennsylvania—a preliminary report. *Proceedings of the Eastern Workshop on Black Bear Management and Research* 4:186–199.
- BATSCHLET, E. 1981. *Circular statistics in biology*. Academic Press, New York, New York, USA.
- BEECHAM, J.J. 1980. Some population characteristics of two black bear populations in Idaho. *International Conference on Bear Research and Management* 4:201–204.
- CLARK, J.D., AND M.R. PELTON. 1998. Management of a large carnivore: black bear. Pages 209–223 in J.D. Peine, editor. *Ecosystem management for sustainability: principles and practices illustrated by a regional biosphere reserve cooperative*. Lewis Publishers, Boca Raton, Florida, USA.
- CLEVENGER, A.P., AND M.R. PELTON. 1990. Pre and post breakup movements and space use of black bear family groups in Cherokee National Forest, Tennessee. *International Conference on Bear Research and Management* 8:289–295.
- EBERHARDT, L.L. 1990. Survival rates required to sustain bear populations. *Journal of Wildlife Management* 54: 587–590.
- ELOWE, K.D., AND W.E. DODGE. 1989. Factors affecting black bear reproductive success and cub survival. *Journal of Wildlife Management* 53:962–968.
- GARSHELIS, D.L., AND E.C. HELLGREN. 1994. Variation in reproductive biology of male black bears. *Journal of Mammalogy* 75:175–188.
- HELLGREN, E.C., AND M.R. VAUGHAN. 1989. Demographic analysis of a black bear population in the Great Dismal Swamp. *Journal of Wildlife Management* 53:969–977.
- , AND ———. 1994. Conservation and management of isolated black bear populations in the southeastern coastal plain of the United States. *Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies* 48:276–285.
- KLENZENDORF, S.A. 2002. Population dynamics of Virginia's hunted black bear (*Ursus americanus*) population. Dissertation, Virginia Polytechnic Institute & State University, Blacksburg, Virginia, USA.
- KOZAK, S.J. 1970. Geology of Elliott Knob, Deerfield, Craigsville, and Augusta Springs Quadrangle. Virginia Division of Mineral Resources, Report of Investigation 21.
- LINDZEY, F.C., AND E.C. MESLOW. 1977. Population characteristics of black bears on an island in Washington. *Journal of Wildlife Management* 41:408–412.
- MILLER, D.A., E.M. HALLERMAN, M.R. VAUGHAN, AND J.W. KASBOHM. 1998. Genetic variation in black bear populations from Louisiana and Arkansas: examining the potential influence of reintroductions from Minnesota. *Ursus* 10:335–341.
- RAWINSKI, T.J., G.P. FLEMING, AND F.V. JUDGE. 1994. Forest vegetation of the Ramsey's Draft and Little Laurel Run Research Natural Areas, Virginia: baseline ecological monitoring and classification. Natural Heritage Technical Report 94-14. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia, USA.
- REYNOLDS, D.G., AND J. BEECHAM. 1980. Home range activities and reproduction of black bears in west-central Idaho. *International Conference on Bear Management and research* 4:181–190.
- ROGERS, L.L. 1977. Social relationships, movements, and population dynamics of black bears in northern Minnesota. Dissertation, University of Minnesota, Minneapolis, Minnesota, USA.
- . 1987a. Factors influencing dispersal in the black bear. Pages 75–84 in B.D. Chepko-Sade and Z.T. Halpin, editors. *Mammalian dispersal patterns*. University of Chicago Press, Chicago, Illinois, USA.
- . 1987b. Effect of food supply and kinship on social behavior, movement, and population growth of black bears in northeastern Minnesota. *Wildlife Monographs* 97.
- SCHWARTZ, C.C., AND A.W. FRANZMANN. 1992. Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. *Journal of Wildlife management* 56:426–431.
- U.S. DEPARTMENT OF AGRICULTURE SOIL CONSERVATION SERVICE. 1965. Land resource regions and major land resource areas of the United States. U.S. Department of Agriculture Handbook 296. U.S. Government Printing Office, Washington DC, USA.
- WHITE, T.H. JR., J.L. BOWMAN, B.D. LEOPOLD, H.A. JACOBSON, W.P. SMITH, AND J.J. VILELLA. 2000. Influence of

Mississippi alluvial valley rivers on black bear movements and dispersal: implications for Louisiana black bear recovery. *Biological Conservation* 95(3):323–331.

WILLEY, C.H. 1974. Aging black bears from first premolar tooth section. *Journal of Wildlife Management* 38:97–100.

WOODING, J.B., AND T.H. HARDISKY. 1994. Home range, habitat use, and mortality of black bears in north-central

Florida. *International Conference of Bear Research and Management* 9(1):349–356.

Received: 13 September 2002

Accepted: 23 June 2003

Associate Editor: J.D.C. Linnell