Demographic Analyses of a Hunted Black Bear Population with Access to a Refuge

ROGER A. POWELL, JOHN W. ZIMMERMAN†, D. ERRAN SEAMAN,*
AND JAMES F. GILLIAM

Department of Zoology, North Carolina State University, Raleigh, NC 27695, U.S.A., email newf@ncsu.edu

Abstract: *Studying one of two bear species not experiencing widespread population decline, provides insight into the population responses of the six bear species that are in decline and into responses of other long-lived species for which data are difficult to collect. Black bear (*Ursus americanus*) sanctuaries were established in North Carolina (U.S.) in 1971 to protect core populations of bears and to provide dispersing bears for hunting. Population index values, derived from counts of bears visiting bait stations, were significantly greater inside the Pisgah Bear Sanctuary than outside and were greater along trails than along roads. Survivorship of bears outfitted with transmitter collars was greater for sanctuary bears alone than for sanctuary plus non-sanctuary bears. Monte Carlo analyses of Leslie matrices showed that the bear population in the sanctuary would be stable if cub survivorship, p_0, was about 0.7, and the population in the sanctuary plus the surrounding area would be stable if p_0 was about 0.83. Estimates of litter survivorship in North Carolina indicate, however, that p_0 can not exceed 0.71. Overall, the matrix analyses indicated an ultimate population decline in the total bear population (sanctuary plus surrounding area). The population index of the bait station did not show a discernible decline. The Pisgah Bear Sanctuary provides dispersing bears for hunters and provides some protection for the resident bears. The sanctuary may not, however, provide resident bears with enough protection to maintain a viable breeding population within its boundaries. Reducing human access to bears and their habitat appears crucial, either by making large sanctuaries or by eliminating roads.*

Analisis demografico de una población de osos negros sujeta a la caza y con acceso a un refugio.

Resumen: *El estudio de los osos negros, una de las dos especies de osos que no ha experimentado una declinacion poblacional generalizada, aumenta nuestra comprensión de las respuestas poblacionales de las seis especies de osos negros que se encuentran en declinación y de otras especies de vida larga para las cuales es difícil recolectar datos. Los santuarios de osos negros (*Ursus americanus*) fueron establecidos en Carolina del Norte (EEUU) en 1971 para proteger las poblaciones centrales de osos y para permitir la caza de aquellos osos que se dispersan. Los valores de los indices poblacionales derivados de los conteos de osos que visitaban estaciones cebadas fueron significativamente mayores dentro del Santuario de Osos de Pisgah que afuera de él y fueron mayores a lo largo de los senderos que a lo largo de los caminos. La supervivencia de los osos equipados con collares transmisores fue mayor en los osos del Santuario que en el conjunto de osos dentro y fuera del santuario. El análisis Monte Carlo usando matrices de Leslie mostró que la población de osos dentro del santuario sería estable si la supervivencia de las crías, P_0, fuera 0.7 y la población total dentro y fuera del santuario sería estable si P_0 fuera 0.83. Sin embargo, las estimaciones de la supervivencia de las crías en Carolina del Norte indican que P_0 no puede exceder 0.71. En general, el análisis matricial indicó una eventual declinación en la población total de osos (que comprende los osos del santuario y aquellos de las áreas circundantes). El índice poblacional de las estaciones cebadas no mostró una declinación clara. El santuario de Osos de Pisgah provee osos que se dispersan para la caza y también proporciona algo de protección a los osos residentes. Sin embargo, el santuario no proporcina a los osos residentes con una protección suficiente como para mantener una población reproductiva viable dentro de sus límites. La reducción del acceso hu-*

*Current address: Olympic National Park, 600 East Park Avenue, Port Angeles, WA 98362, U.S.A.
†Current address: Mt. St. Clare College, 400 N. Bluff Blvd., Clinton, Iowa 52327, U.S.A.
Paper submitted October 14, 1994; revised manuscript accepted February 27, 1995.

mano a los osos y su principal hábitat parece ser crucial, esta se debe lograr ya sea mediante la creación de grandes santuarios o la eliminación de rutas.

Introduction

Six of the eight species of bears in the world are experiencing significant population declines, and the future for five of these species is uncertain at best (Servheen 1989). Although the status of the North American black bear (*Ursus americanus*) is generally secure, some isolated populations in the southern and southeastern sections of the U.S. are not (Pelton 1982; Servheen 1989). The black bear was listed in 1972 and again in 1987 as a "species of special concern" in North Carolina (Collins & Hamilton 1977; Powell 1987; by state law no game species can be declared threatened or endangered). Because black bears are potentially long lived, understanding a population requires the long-term research that is not possible with many endangered species. Study of black bears and interactions between humans and black bears can provide insight into other bear species and other long-lived, endangered species for which we have few data.

Black bear sanctuaries were established in North Carolina in 1971 by the North Carolina Wildlife Resources Commission to insure the survival of black bears and to provide for the continued production of a harvestable surplus of bears for sport hunting. When the sanctuaries were established, information on sanctuary use by bears and on the dynamics of sanctuary populations was not sufficient to assess whether the sanctuary system could meet program goals (Sanders et al. 1978; Betton 1982; Warburton 1984). A thorough assessment of the effec-

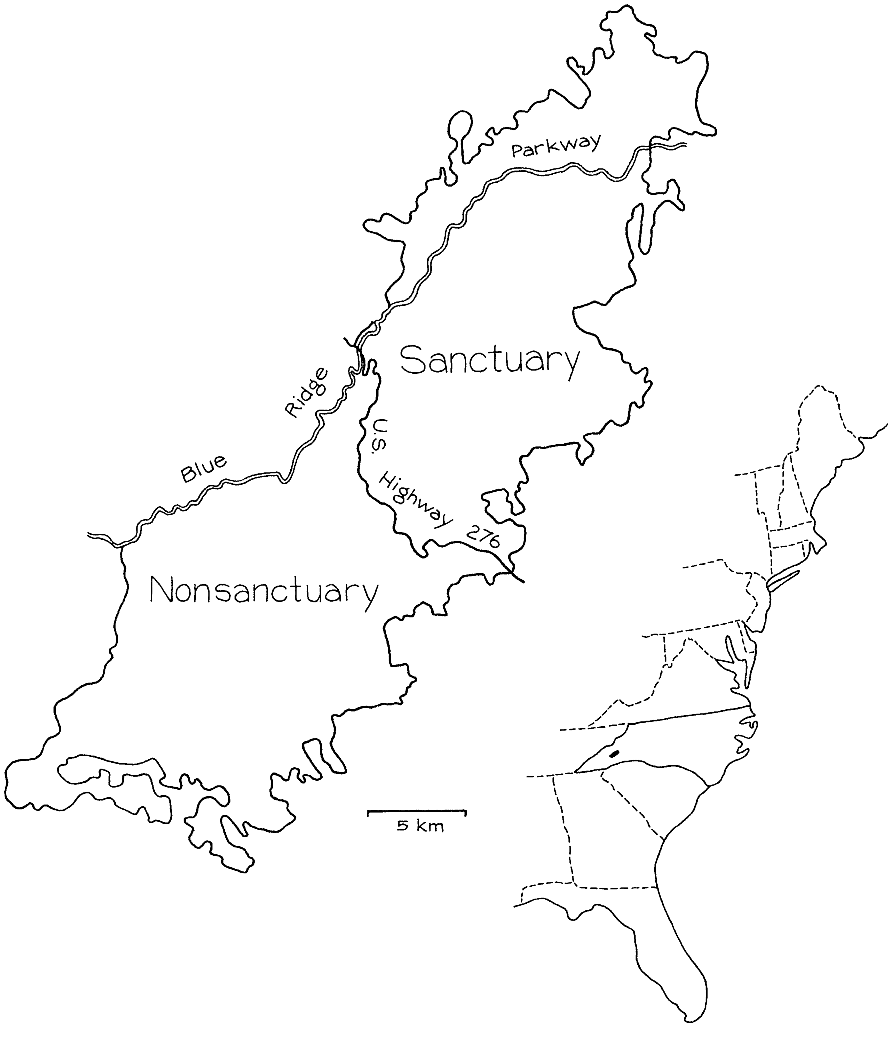

Figure 1. Map of the study area, the Pisgah Bear Sanctuary, and adjacent Pisgah National Forest land in North Carolina.

tiveness of the sanctuary system was needed. We evaluated the demographic characteristics of the bear population in the Pisgah Bear Sanctuary, the largest black bear sanctuary in the North Carolina system, and the surrounding area.

Methods

Study Area

We conducted our study from May 1981 through December 1990 in the Pisgah Bear Sanctuary and adjacent nonsanctuary lands located within the Pisgah National Forest, approximately 35 km southwest of Asheville, North Carolina (Fig. 1). The sanctuary and the nonsanctuary areas together total over 400 km^2 and are located in the southern Blue Ridge Mountains. Elevations range from 650 to 1750 m. The Blue Ridge Parkway runs along Pisgah Ridge at approximately 1500 m, above most of the study area. The area was managed for multiple use, including timber, wildlife, and recreation. Bear hunting was illegal within the sanctuary and along the Blue Ridge Parkway corridor.

Precipitation was frequent in the study area, and heavy fog often enveloped high elevations. Predominant trees were hardwoods, such as oaks (*Quercus* sp.), hickories (*Carya* sp.), tulip poplar (*Liriodendron tulipifera*), and maples (*Acer* sp.), intermixed with pine (*Pinus* sp.) and hemlock (*Tsuga* sp.). Betton (1982) provides details on the forests in the Pisgah Bear Sanctuary and on adjacent U.S. Forest Service lands.

Bait Station Population Index

Starting in 1981 we set 68 bait stations each year in the Pisgah Bear Sanctuary and in the adjacent nonsanctuary study area (Johnson & Pelton 1980; Betton 1982). In each area we set over 40 stations at 0.8-km intervals along designated trails and over 25 stations along designated roads; we matched trails and roads for elevation and forest type between the two areas. Two sardine cans were nailed to a tree at head height at each bait station then punched open with the hammer claw. Bait stations were not visible from the trails or roads. After 5 days (occasionally 6–7 days) bait stations were revisited. Stations visited by bears were noted and all cans were removed. We determined each year's index as the number of bear visits per station per day.

We indexed the population in late June and early July in 1981–1982 and in mid-May in 1983–1985 to facilitate trapping. Beginning in 1986 we indexed the population both in mid-May and in late June and early July to document differences. We adjusted results for 1983–1985 by the mean ratio of June-July results to May results.

Trapping and Telemetry

We trapped bears in Aldrich foot snares modified for bear safety (Johnson & Pelton 1980) or in culvert traps. After 2 years with no captures outside the sanctuary despite more than 200 trapnights each year, we confined trapping to the sanctuary beginning in 1986. We immobilized bears with a mixture of freeze-dried ketamine hydrochloride reconstituted in xylazine (200 mg ketamine + 100 mg xylazine/cc) or freeze-dried ketamine hydrochloride and freeze-dried xylazine reconstituted in carbocaine (200 mg ketamine + 100 mg xylazine/cc of 1% carbocaine; Cook 1984), administered with a jab stick or blow gun at a dosage of 1 cc/25 kg estimated weight. We tagged, tattooed, and measured bears and extracted a first upper premolar from each to estimate age. Trap density was highest near the Blue Ridge Parkway. Bears used high-elevation areas most heavily (Betton 1982), and the parkway was at high elevations. Therefore, our sampling of bears was biased similarly to bear use of the study area.

We trapped 110 bears (70 males, 39 females, 1 sex unknown) and outfitted 67 (36 males, 31 females) with 800-g motion-sensitive radiotransmitter collars, ear tag transmitters (Telonics, Mesa, Arizona) or 900-g transponder collars (3M, St. Paul, Minnesota; Wildlink, Brooklyn Park, Minnesota). Whenever possible, we followed bears to their dens to change collars or replace batteries.

Before 1987 we outfitted all bears with Telonics transmitters broadcasting in the 150–152 mHz range. From January 1987 through early June 1988 we removed transmitters from bears because poachers were using telemetry equipment to locate bears (Powell et al. 1992).

From June 1988 through 1990 we outfitted seven juvenile bears (1.5–3.5-year-old males, two 1.5–2.5-year-old females) with motion-sensitive, breakaway transmitter collars that transmitted on a previously unused frequency band not monitored by poachers. Ten adult bears (four males, six females) were outfitted with transponder collars whose signals could be programmed to turn on and off at designated times or upon receipt of a coded signal.

We located bears using Telonics receivers and an eight-element Yagi antenna mounted on a truck or occasionally on foot using a two- or three-element antenna. In the field we mapped compass line bearings on USGS topographic maps (1:24,000) to estimate bear locations and to aid in choosing telemetry stations. Bear locations were estimated from triangulation of compass bearings taken from at least three different stations within 15 minutes. In 1981–1982 and 1986–1990 we located bears at 2-hour intervals for 8-hour periods staggered to begin at 32-hour intervals, as permitted by the trapping schedule. This schedule eliminated autocorrelation between 8-hour periods and balanced the bias within each 8-hour period. In 1983–1985 we located bears at 2-hour intervals, for 24 hours at the beginning of each week and at 2-hour intervals for 12 hours (beginning before sunrise to determine sleeping sites) at the end of each week. Thus, each bear ideally had two to five sets of 4, 6, or 12 locations each week.

We estimated telemetry error by triangulating on test collars placed in locations unknown to the researchers and by triangulating on bears whose dens were subsequently located. Each researcher took compass bearings on a test collar (range 0.3–5.0 km from the receiver) at least once during each telemetry session. We treated all test collar data the same as bear data.

A computer program triangulated location data used in analyses. Estimated locations were the intersections of two compass bearings or the arithmetic means of intersections of three or more compass bearings. For 1986–1990 our triangulation program allowed deletion of specific intersections of compass bearings (for example, the intersection of two nearly parallel lines were deleted, but the intersections of each with other bearings were retained). Zimmerman (1992) and Zimmerman & Powell (1995) demonstrated that these triangulation methods were at least as accurate as those using the Lenth estimator.

If the geometric mean center of a bear's estimated locations was located within the Pisgah Bear Sanctuary, we considered the bear to be a sanctuary resident. Centers and bear activity tended to be clearly inside or outside the sanctuary.

Survivorship Estimates

We could not estimate survivorship from the age structure of harvested bears because we could not assume that the population was stationary (Caughley 1977). Therefore, we calculated the proportion of radio-tagged bears surviving from each age to the next, p_x ($\pm$ SE calculated as for binomial distributions), for each age (year) class beginning at age 1 year (Caughley 1977). This method requires neither a stable population size nor a stable age distribution but assumes that the sample of deaths is representative of the population. Using data for all years and nested subsets of data, we calculated three estimated p_x survivorship schedules: (1) Survivorship from one live-trapping season to the next (one year later) for bears resident in the Pisgah Bear Sanctuary who had worn radio transmitters continuously from one trapping season to the next. We considered bears to have died only if they were harvested and reported to the North Carolina Resource Commission, if their bodies were found in the woods, or if their transmitters were found under conditions indicating the bear had been poached (for example, bear not reported as harvested and its cut collar found in the woods or river or found with a bullet hole in transmitter). (2) Survivorship calculated as above but without regard to sanctuary residency. (3) Survivorship calculated as above but including as deaths those bears not known to have died but strongly suspected of having been killed (for example, multiple sources of anecdotal evidence coincided with telemetry data on a bear's last location or disappearance of bear coincided with known hunter activity).

Method 1 was applied to sanctuary residents only. If survivorship differed between sanctuary residents and nonresidents, then method 2 showed the direction of the difference but may not have been representative of survivorship for bears in the Mt. Pisgah region, because most of the bears studied lived predominantly in the sanctuary. Excluding suspected poaching in calculations of survivorship probably biased calculations the first two estimates to be too high, but it guaranteed that bears were not mistakenly presumed dead. Including bears suspected of being poached, the third method, included some anecdotal information and revised survival estimates downward.

We followed 51 radio-tagged bears for 89 bear years. Bears whose transmitter signals were lost for unknown reasons (such as possible collar failure or long-distance dispersal) were not used in calculating survivorship in the year they disappeared. These bears provided esti-

Table 1. Mean survivorship, p_x (survivorship from age x to age $x + 1$), and fecundity, m_x (fecundity of females of age x), for bears in the Pisgah Bear Sanctuary and adjacent areas.

Bear age (years)	Survivorship: Sanctuary p_x SE	n	Sanctuary + nonsanctuary p_x SE	n	Including suspected poaches p_x SE	n	Fecundity m_x[a]
1	0.73 ± 0.13	11	0.75 ± 0.14	12	0.75 ± 0.14	12	0.00
2	0.83 ± 0.11	12	0.73 ± 0.12	15	0.69 ± 0.12	16	0.04
3	0.67 ± 0.12	15	0.62 ± 0.12	16	0.53 ± 0.13	19	0.64
4	0.57 ± 0.19	7	0.67 ± 0.15	9	0.60 ± 0.16	10	0.78
5	0.67 ± 0.27	3	0.60 ± 0.22	5	0.60 ± 0.22	5	0.71
6+[b]	0.76[c] ± 0.11	14	0.73[c] ± 0.12	15	0.58[c] ± 0.13	19	0.77

[a] *m_x was calculated from harvest data of Collins (1977–1990).*
[b] *p_x for ages ≥6 was assumed to be the same.*
[c] *p_{6+} calculated without using the female strongly suspected of having been poached equaled 0.83, 0.76, and 0.59.*

mates of p_x for ages 1 year or older. We calculated a single p_x value for all bears ages 6 years and older because it was reasonable to expect relatively constant survivorship for adult bears. Survivorships calculated for females alone were lower than those for males. Males should have lower survivorship because they are the dispersing sex and are more vulnerable to hunting. We suspect that low female survivorship resulted from random sampling error due to small sample sizes; therefore, we combined data for females and males to estimate survivorships (Table 1).

We could not calculate survivorship from birth to age 1 (p_0) from telemetry data. We estimated cub survivorship in three ways to obtain a range of potential values. First, we calculated the proportion of cubs that we tagged as newborns and recaptured at age 1 or older. Second, we calculated the proportion of litters born to collared bears for which we documented survival or could infer from the mother's behavior that some cubs survived. These two estimates were hampered by small sample sizes, and the latter estimated litter survival rather than cub survival. Third, we calculated the proportion of female bears harvested each year from 1976 through 1989 that did not breed in two successive years (calculated from corpora lutea and placental scar data reported by Collins 1977–1990). A complete reproductive cycle takes 2 years for female black bears, and females who lose their litters before the summer breeding season will breed in two successive years. This estimate applied to all females in the North Carolina mountains, not just the Pisgah Bear Sanctuary and its surrounding area. Also, it was biased to overestimate survivorship of litters and p_0 because females will breed at two-year intervals even if some but not all cubs die and if cubs die after the breeding season. Thus, this estimate is an upper limit to true cub survivorship.

Fecundity Estimates

We estimated fecundity (m_x) from North Carolina Wildlife Resource Commission data on reproductive tracts of female bears harvested in 1976–1989 (Collins 1977–1990). We used these data because we know of no reason why fecundity should differ between bears in the Pisgah Bear Sanctuary and bears elsewhere in the mountains of North Carolina and because we handled few litters. Females who reproduce successfully give birth to litters every 2 years, usually producing their first litters at age 3 or 4. The proportion of 2.5-year-old females having placental scars was calculated and used as the estimated probability of having cubs at that age (Pr_2). The probability was multiplied by 0.5, the average litter size for that age (because of the convention of using only females in demographic calculations), to estimate fecundity at that age. The probability of producing cubs at the next age (Pr_3) was estimated as

$$Pr_3 = [Pr_2 \cdot F_2 + (1 - Pr_2)],$$

where F_2 is the failure rate for reproductive females 2.5 years old (the proportion of females producing litters 2 years in a row because the first litter was lost). The probability of producing cubs in succeeding years was calculated as

$$Pr_x = [Pr_{x-2}(1 - F_{x-2}) + Pr_{x-1} \cdot F_{x-1}],$$

where Pr_x is the probability of producing cubs at age x and F_x is the failure rate for reproductive females age x.

Monte Carlo Calculations

A Leslie matrix (Gurney et al. 1983; Leslie 1945, 1948) was constructed for each of the three p_x schedules, but cub survivorship was considered unknown. Therefore

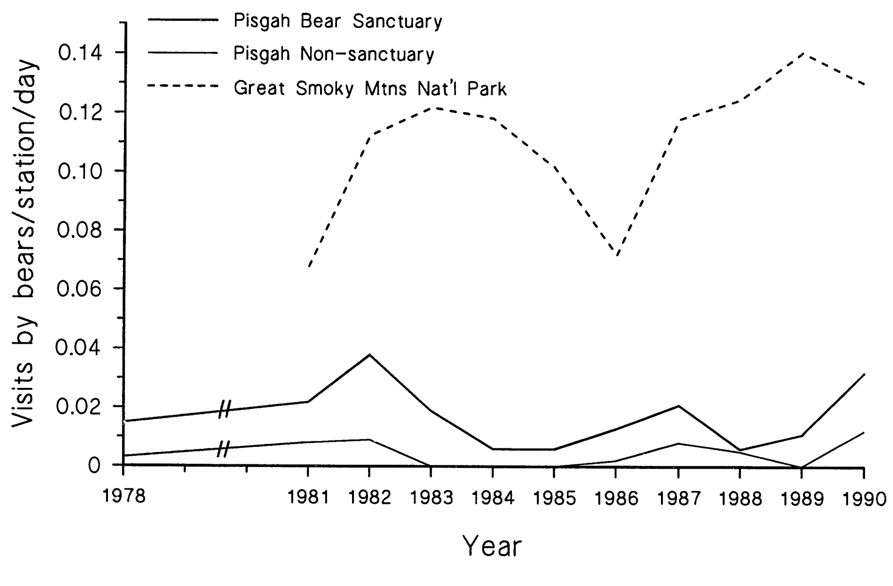

Figure 2. Bear visits per bait station per day for the Pisgah Bear Sanctuary and nonsanctuary study area, 1978 and 1981–1990, and for Great Smoky Mountains National Park.

we first explored the relationship between cub survivorship and lambda, λ, the annual rate of population increase, using Monte Carlo population simulations for each p_x schedule. For a given cub survivorship (p_0 = 0.1, 0.2, . . ., 1.0) and p_x schedule, random numbers were drawn from the distributions for each p_x, m_x, and F_x, where a given distribution's mean and standard deviation were the estimated mean and standard error for the given parameter. λ was calculated for the matrix. New sets of random numbers were drawn, λ was calculated repeatedly to achieve estimates of all statistics (stable to two decimal places), and the following statistics were calculated: mean λ, SE of λ, 95% confidence interval for λ, proportion of λs > 1, and proportion of λs > 0.978. The value of 0.978 was chosen as a λ that would lead to a detectable decrease in the bear population: A population with λ = 0.978 is expected to exhibit a 20% decline over 10 years (0.978^{10} = 0.80). Finally, for cub survivorship estimated from female reproductive tracts, we examined the implications of the simulation results for bears in the Pisgah Bear Sanctuary and the surrounding area.

These matrix analyses apply to a closed population. Because the bear population in the Pisgah Bear Sanctuary was not closed, we interpreted the results of the matrix analyses in the light of what we knew about dispersal.

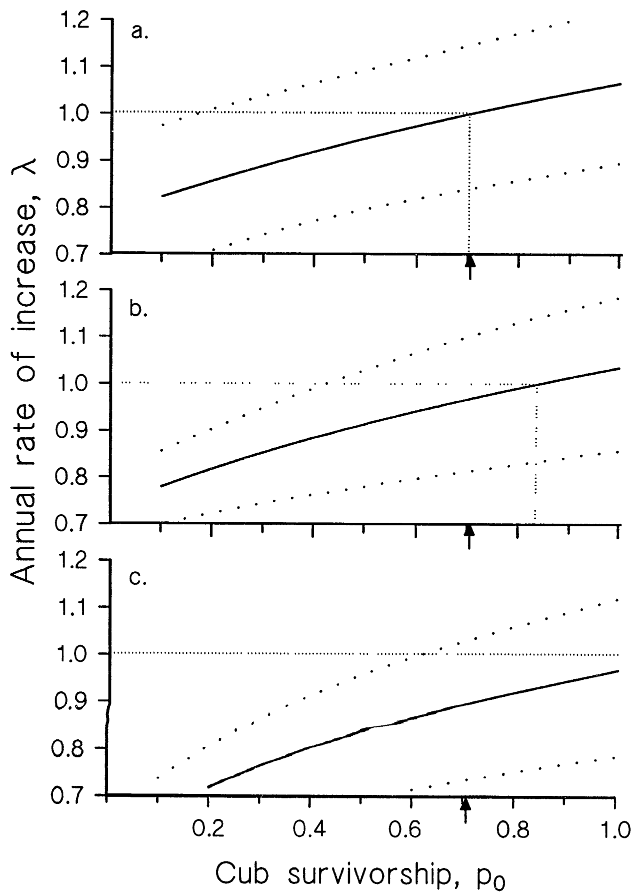

Figure 3. Estimated annual rate of increase, λ, and 95% confidence limits on λ for cub survivorship, p_0, *varying from 0.1 to 1.0: estimated from data on known deaths of bears who wore transmitters and were resident in the Pisgah Bear Sanctuary (a), estimated from bears resident in the sanctuary and from nonresidents (b), estimated from data on sanctuary residents and nonresidents, including as deaths those bears suspected as having been poached (c). Arrow marks maximum cub survivorship possible, given the documented rate of litter failure.*

Results

Bait station indices for the Pisgah Bear Sanctuary were greater than for the nonsanctuary study area (paired *t*-tests, data paired by year, $p < 0.001$; Fig. 2). Bait station indices averaged 1.55 times greater in late June and July than in May. Bait stations on trails were visited by bears significantly more often than those along roads both inside and outside the sanctuary (paired *t*-tests, $p < 0.01$ for each). The slope of a linear regression of the Pisgah Bear Sanctuary data on year was negative but not significantly different from zero.

Of 25 collared bears known to have died, 14 (possibly 13) were killed legally by hunters, 9 (possibly 10) were killed illegally, and 2 died of other causes (1 unknown, 1 drowned). Survivorship estimates, p_x, are presented in Table 1. Ten collared bears killed legally were considered sanctuary residents for at least 1 year. Four of these bears dispersed and established home ranges outside the sanctuary, and 6 were killed in small parts of their home ranges that extended beyond sanctuary boundaries. Four of these latter 6 were adult bears (2 males, 2 females), and the remaining two were 3.5-year-old males that were not dispersing to new home ranges outside the sanctuary.

Twelve collared bears (all females) located more than 40 times were never known to have left the sanctuary. Six wore transmitters for 2 years or more. One was poached, and five were suspected to have been poached.

The upper limit to cub survivorship (p_0) calculated from data for the reproductive tracts of harvested female bears was 0.71. Estimates of p_0 from data on collared bears were 0.27 (± 0.13) and 0.50 (± 0.25). The latter two estimates were derived from small samples (11, 4), and the former is an upper limit rather than a true estimate of p_0.

Table 1 shows fecundity calculated from data gathered by Collins (1977–1990) for harvested bears. Approximately one-half of the bears harvested at age 3.75 years had produced cubs the previous winter. Average litter

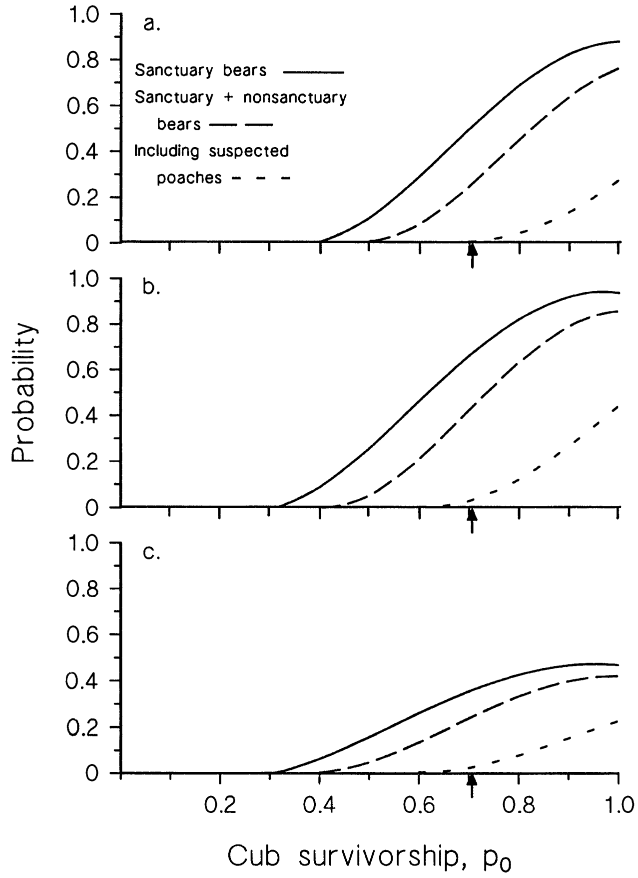

Figure 4. Estimated probabilities that the annual rate of increase, λ, for the bear population in the Pisgah Bear Sanctuary and surrounding area indicates that the population is stable, increasing, or decreasing for cub survivorship, p_0, varying from 0.1 to 1.0: the probability that λ > 1 (a), the probability that λ > 0.978 (λ = 0.978 corresponds to a 20% decline over 10 years)(b), the probability that λ > 0.978 given that λ < 1 (c). Arrow marks maximum cub survivorship possible, given the documented rate of litter failure.

size for females aged 3 years was 2.4 (± 0.9). Litter size of older females was 2.6 (± 0.8). These litter sizes are not statistically different but, because they probably reflect a biologically significant difference, the two different litter sizes were used to create Table 1. In our study females older than 5 years always produced litters of three cubs. The failure rate for females 4.75 years and older (the proportion that had both corpora lutea and placental scars, indicating loss of litter between birth and the breeding season) was 0.29. Only one published report exists of wild female black bears successfully producing cubs 2 years in a row (LeCount 1983), and we have no such evidence for bears in our study area. Therefore, this estimate of failure rate is not likely to be biased.

Figure 3 shows how λ changes with cub survivorship, p_0, the only survivorship we could not estimate from field data. Lambdas and associated 95% confidence limits were calculated from over 500,000 Monte Carlo population simulations using population matrices whose elements are listed in Table 1. For the population matrix generated from data for sanctuary bears only, $\lambda = 1$ for p_0 slightly greater than 0.70. Using data for sanctuary plus nonsanctuary bears, $\lambda = 1$ for $p_0 \approx 0.83$. When data includes suspected poaches, λ never reaches 1, even when cub survivorship is 1. Because the litter failure rate was 0.29, cub survivorship can not exceed 0.71.

Figure 4a shows the probability that the bear population is stable or increasing ($\lambda > 1$). Figure 4b shows the probability that the population is increasing or decreasing at a rate difficult to detect ($\lambda > 0.978$). Figure 4c shows the probability that a bear population with $\lambda < 1$ will not have its population decrease detected because the decrease occurs slowly.

Sensitivity (s $\delta\lambda/\delta y$, where y is some parameter in the Leslie matrix) and elasticity analyses (e, $[\delta\lambda/\delta y]\cdot[y/\lambda = \delta\ln\lambda/\delta\ln y$) (Caswell 1978; Stearns 1992) showed that populations described by the matrices would be most affected by absolute (s) and proportional (e) changes in p_0 ($s = 0.25$, $e = 0.18$), p_1 ($s = 0.23$, $e = 0.18$), and p_2 ($s = 0.23$, $e = 0.17$). The populations would be less affected by changes in fecundity ($s = 0.09$, $e = 0.13$).

We were unable to collect sufficient demographic data for bears residing outside the Pisgah Bear Sanctuary to analyze this population separately. Differences in Table 1 and Figs. 3 and 4 between sanctuary and sanctuary plus nonsanctuary populations are caused by bears not resident in sanctuary.

Discussion

The bait station index values within the Pisgah Bear Sanctuary were higher every year than those collected outside the sanctuary in adjacent and similar national forest land (Fig. 2). We believe that these statistically significant results represent real differences in the bear population densities, indicating that the Pisgah Bear Sanctuary provides some protection for its bears.

The difference between bait stations set on trails and those set on roads indicates that bears in both the Pisgah Bear Sanctuary and in the adjacent national forest avoided roads. Similar results have been reported by Hamilton (1978), Hugie (1982), Quigley (1982), Hellgren (1988), Brody and Pelton (1989), and Beringer et al. (1990). At least two adult female bears in this study were shot illegally near roads, indicating the roads may pose a serious threat to bears in the sanctuary. Another female disappeared the first day of deer season in the first fall after a new logging road was built into her home range.

The black bear population index in the Pisgah Bear Sanctuary rose distinctly during the two summers of 1989 and 1990 following Operation Smoky—a law enforcement effort to stop poaching (Fig. 2)—and we did not document any poaching or unexpected bear disappearances from August 1988 until the autumn of 1991. These data suggest that Operation Smoky depressed the poaching level in the Pisgah Bear Sanctuary and surrounding areas for at least a few years. This conclusion must be made cautiously because yearly changes in population index values were influenced by weather and other environmental conditions as well as by bear population density. The population index is best used to make within-year comparisons of two or more similar study areas or to indicate long-term population trends.

The life-table analysis also indicated that the Pisgah Bear Sanctuary protected bears. Survivorships (p_x) and annual rates of population growth (λs) calculated from data on sanctuary residents are greater than those calculated for all bears wearing transmitters, regardless of place of residence (Table 1, Figs. 3 & 4). Survivorships of bears not resident in the sanctuary are probably considerably lower than survivorships shown in Table 1 for sanctuary plus nonsanctuary bears. The great majority of the bears outfitted with transmitters in this study were residents of the sanctuary. Therefore, the survivorships calculated for all bears studied are biased toward the survivorships of sanctuary bears.

Table 1 and Figs. 3 and 4 present survivorship data for both male and female bears, in contrast to the convention of addressing females only. Because dispersing male bears are often harvested, we expected male survivorship to be lower than female survivorship. Estimated survivorships for females, however, were lower than those for males. This may have been a sampling error resulting from small sample sizes, or female survivorship may truly have been low due to the biased sex ratio in poached bears. Six female bears were known to have been poached, but only three males were poached. An additional five females were suspected to have been poached, but only four males were suspected poaching victims. Females have smaller home ranges and therefore when running may return to poachers' locations sooner than males do, or females may be easier to locate than males. If female survivorship is truly lower than male survivorship, our calculations overestimate p_x, λ, and the viability of the Pisgah bear population.

Estimating p_0 is critical to understanding the population dynamics of the bear population in the Pisgah Bear Sanctuary. We believe that survivorship of 0.71, calculated from harvest data gathered by Collins (1977–1990), is a reasonable upper limit for survivorship of cubs for all years in the Pisgah Bear Sanctuary. Estimates of cub survivorship generated from trapping and other data were considerably lower (0.27, 0.50) but were subject to error from small sample sizes. These values encompass a large range, yet both 0.71 and one of the lower values may be correct because they actually represent survivorship to different ages. The higher value represents survivorship of at least one cub from a litter to roughly age 0.75 years. The lower values represent survivorship to age 1–1.25 years. It is possible that approximately 70% of cubs survive through their first summer but only 25–50% of them survive the following winter. The period between these two estimates comprises a cub's first winter when it is dependent on fat it has acquired during the previous active season. In addition, the 0.71 value was derived from the reproductive tracts of females that were harvested during autumn, meaning that their cubs had a lower probability of surviving through the winter than cubs whose mothers lived.

Reported values of p_0 for black bears range from 0.12 to 0.95 but are commonly around 0.7 (Jonkel & Cowan 1971; Rogers 1977; Wathen 1983; Bunnell & Tait 1985; LeCount 1987). The low values reported for p_0 were for study areas with low productivity or for years with poor food. The sanctuary had high productivity of some important foods; although food crops are sometimes very poor, they appear never to fail completely (Beck & Olson 1968; Beck 1977; Powell & Seaman 1990). Thus, if survivorship of cubs in the Pisgah Bear Sanctuary is based on nutrition, it ought to be high.

We believe that the m_x table (Table 1) calculated from the large sample of reproductive tracts of harvested bears probably provides a good estimate of black bear fecundity in the North Carolina mountains in general, including the Pisgah Bear Sanctuary. This reproductive output compares favorably with that reported elsewhere (Rogers 1976, 1987; Bunnell & Tait 1981; Alt 1989; Kolenosky 1990) and exceeds that reported for all studies but one (Alt 1989), which is consistent with the low-density bear population in our study area and the abundance of food (Powell & Seaman 1990). In addition, small differences in fecundity that may occur between bears in our study area and bears in other areas in the North Carolina mountains should have had little effect on our results. Sensitivity and elasticity analyses showed that our population would be less affected by changes in fecundity than by changes in early survivorship.

The demographic data (Table 1, Figs. 3 & 4) indicate that a closed bear population in the Pisgah Bear Sanctuary was expected to be stable if cub survivorship was near the maximum possible of 0.71. For $p_0 = 0.70$ the population has a 50% chance of being stable or increasing. The population is not closed, however, and bears disperse into and out of the sanctuary. The bait station index data clearly show that bear densities are higher within the sanctuary boundaries, and the sanctuary system is based on the premise that dispersal out of a sanctuary will exceed dispersal into it. We documented dispersal out of the Pisgah Bear Sanctuary but could not quantify dispersal into the sanctuary. We believe it is safe to conclude that dispersal from the sanctuary equaled or exceeded dispersal into it. Thus, the bear population in the sanctuary differed from a closed population by having net emigration. If emigration exceeds immigration and if $p_0 < 0.70$, then the demographic data indicate that the bear population in the Pisgah Bear Sanctuary may not be stable but decreasing. This conclusion appears to contradict the population index data, which are consistent with the null hypothesis of no net population change (Fig. 2). Weather or other factors may have affected the population index, hiding a decline, but the length of this study minimizes the effects of factors that affect single years. The demographic analyses may have underestimated female survivorship due to small sample sizes or other, unknown sources of error.

More important, the apparent contradiction between conclusions from the demographic analyses and the population index data may be explained by the age distribution of the bear population. The predictions from the demographic data are valid for a population with a stable age distribution. Populations with unstable age distributions may behave differently in the short term but will behave as predicted after a delay. Harvest data (Collins 1977–1990) indicated that the age distribution during this study for bears throughout the North Carolina mountains was biased from stable proportions toward early breeding ages. In addition, the proportion of 1.5- and 2.5-year-olds breeding in this population increased significantly between 1976 (25%) and 1989 (88%; $p < 0.06$ for 2.5-year-olds; $p = 0.05$ for 1.5- plus 2.5-year-olds; SAS regression analysis). Therefore, the population in the Pisgah Bear Sanctuary may not have decreased during the study, in agreement with the population index data, but may decrease in the future, in agreement with the demographic analyses.

We combined data for sanctuary residents and nonresidents to gain a picture of the demographics of the bear population in the Mt. Pisgah area. Analyses of these data indicate that a closed bear population would not be stable and would be decreasing or would decrease in the future, depending on its age distribution. We do not know whether dispersal into the Mt. Pisgah area is balanced by dispersal out of the area. Our analyses suggest that the bear population in the sanctuary plus the surrounding area can be stable in the long term only in the unlikely event that it is augmented by dispersal of bears into the area.

Management Implications

Managing for sanctuary goals requires $\lambda > 1$. The most effective way to increase λ for the bear population in the Pisgah Bear Sanctuary is to increase survivorship of bears to more than 3 years. The parameters in the Leslie matrix with greatest sensitivity and elasticity were p_0, p_1 and p_2. Approximately one-third of the known mortality of collared bears in the Pisgah Bear Sanctuary was from poaching. Had this source of mortality not existed, it is possible that survivorship would have been significantly greater. Cub survivorship needs to be estimated more accurately. If it is 0.70 or less, survivorship of all age classes, especially bears less than 3 years old, must be raised. Our analyses indicate that there is only a narrow window of cub survivorship ($0.70 < p_0 < 0.71$) for which the bear population in the Pisgah Bear Sanctuary might approach demographic stability.

Assuming that cub survivorship is roughly 0.7, our best estimates of λ have 95% confidence intervals that include 1.00 for data taken from sanctuary residents and for residents plus nonresidents (Fig. 3). For data including suspected poaches, however, the 95% confidence interval for λ barely reaches 1.00. If we are conservative statistically in interpreting these data and analyses and most concerned with Type I error (rejecting a null hypothesis that is true), then our population index data and demographic data do not allow us to reject the hypothesis that the bear population in the Pisgah area was stable and will remain stable as long as the conditions experienced during our study continue. If we are most concerned with minimizing Type II error (accepting a null hypothesis that is false), then our data indicate at least a 50% chance that an unstable age distribution during the study explains the current steadiness of the bait station index results. The data also suggest a long-term population decrease (Figs. 3 & 4). There is a 30% chance that the population decrease will be substantial ($\lambda < 0.978$). Because the risks associated with not perceiving a population decline are greater than those for not perceiving a population increase, we believe that it is best to minimize Type II error. This indicates that even a 10-year study may not be long enough for long-lived species such as black bears.

Larger sanctuary size might increase survivorship for bears. Great Smoky Mountains National Park, approximately 50 km west of the Pisgah Bear Sanctuary, is approximately four times larger and has significantly higher bait station index values (Fig. 2; Johnson 1987, 1990). The park also has a lower density of roads, however, which influence bear behavior and provide access to poachers. For sanctuaries smaller than the Pisgah Bear Sanctuary, increased size may increase survivorship for resident bears. For sanctuaries as large or larger than the Pisgah Bear Sanctuary, reducing road density may be more important.

In summary, the Pisgah Bear Sanctuary clearly provides its resident bears with some protection. During the 10 years of this study the bear population density within the sanctuary, as measured by the bait station index and trapping results, was significantly higher than the density outside the sanctuary (Fig. 2). Survivorship of bears within the sanctuary was higher than that for bears outside the sanctuary (Table 1, Figs. 3. & 4). The sanctuary also produced bears that dispersed beyond its boundaries to be hunted. Thus, the Pisgah Bear Sanctuary partially meets its goal by providing protection for its resident bears and providing dispersing bears for hunters.

The sanctuary may not, however, provide its resident bears with enough protection to maintain a viable, core breeding population within its boundaries. Also, a population matrix analysis should show that the sanctuary bear population has demographic characteristics consistent with significant long-term increase, thus providing many dispersing bears and balancing hunting mortality outside the sanctuary.

Sanctuaries appear to be a good means of managing black bears, and the Pisgah Bear Sanctuary meets its goals in part. This has a significant and positive effect on the black bear population in the North Carolina mountains. The effect, however, may not be great enough to produce a stable or increasing bear population, given the low survivorship of bears in the sanctuary and the surrounding area. Decreasing human access to bears and their habitat appears crucial, either by making sanctuaries larger or, especially, by eliminating roads. Efforts to increase survivorship will be most effective if young bears (< 3 years of age) are targeted.

Acknowledgments

Graduate students Mike Fritz, Peggy Horner, John Noel, and Gordie Warburton developed associated research projects and helped collect data. Numerous students, volunteers, and approximately 200 Earthwatch volunteers assisted with field work. Dick Lancia, Russ Lande, and Ken Pollock commented on previous drafts of this paper. Financial and logistic support was provided by Robert Bacon, Citibank Corp., Earthwatch/The Center for Field Research, Federal Aid in Wildlife Restoration Project W-57 administrated through the North Carolina Wildlife Resources Commission, Ginger and Dick King, McIntire Stennis funds, the National Geographic Society, the National Park Service, the National Rifle Association, National Science Foundation grant DEB-92-21788, the North Carolina Agricultural Research Service, North Carolina State University, Port Clyde and Stinson Canning Companies, 3M Co., the U.S. Forest Service, the Wildlands Research Institute, Wil-Burt Corp., and Wildlink, Inc.

Literature Cited

Alt, G. L. 1989. Some aspects of female black bear reproductive biology in northeastern Pennsylvania. Page 48 in R. Archibald, T. Hamilton, G. Jones, D. Robinson, D. Caldwell, L. Darling, R. McLaughlin, L. Steele, F. Bunnell, editors. Future for bears, abstracts of the 8th International Conference on Bear Research and Management. International Association for Bear Research and Management, Victoria, British Columbia.

Beck, D. E. 1977. Twelve-year acorn yield in Southern Appalachian oaks. Research note SE-244. U.S. Forest Service, Asheville, North Carolina.

Beck, D. E., and D. F. Olson. 1968. Seed production in Southern Appalachian oak stands. Research note SE-91. U.S. Forest Service, Asheville, North Carolina.

Beringer, J. J., S. G. Seibert, and M. R. Pelton. 1990. Incidence of road crossings by black bears on Pisgah National Forest, North Carolina. International Conference on Bear Research and Management. **8:** 85-92.

Betton, R. 1982. The use of activity indices to evaluate black bear sanctuary utilization. M.S. thesis. North Carolina State University, Raleigh.

Brody, A. J., and M. R. Pelton. 1989. The effects of roads on black bear movements in western North Carolina. Wildlife Society Bulletin **17:** 5-10.

Bunnell, F. L., and D. E. N. Tait. 1981. Population dynamics of bears—implications. Pages 75-98 in C. W. Fowler, and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York.

Bunnell, F. L., and D. E. N. Tait. 1985. Mortality rates of North American bears. Arctic **38:**316-322.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology **14:**215-230.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, London.

Collins, J. M. 1977-1990. Study B1—Status of black bear in North Carolina. Annual performance reports, federal aid in wildlife restoration, vols. 30-43. North Carolina Wildlife Resources Commission, Raleigh.

Collins, J. M., and J. Hamilton. 1977. *Ursus americanus* Pallas. Pages 400-402 in J. E. Cooper, S. S. Robinson, and J. B. Funderburg, editors. Endangered and threatened fauna and flora of North Carolina. North Carolina Museum of Natural History, Raleigh.

Cook, B. 1984. Chemical immobilization of black bears in Great Smoky Mountains National Park. Eastern Black Bear Workshop **7:**79-81.

Gurney, W. S. C., R. M. Nisbet, and J. H. Lawton. 1983. The systematic formulation of tractable single-species population models incorporating age structure. Journal of Animal Ecology **52:**479-495.

Hamilton, R. J. 1978. Ecology of the black bear in southeastern North Carolina. M.S. thesis. University of Georgia, Athens.

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

Hugie, R. D. 1982. Black bear ecology and management in the northern conifer-deciduous forests of Maine. Ph.D. thesis. University of Montana, Missoula.

Johnson, K. G., editor. 1987. Annual progress report—1987: Bait-station surveys to determine relative density, distribution, and activities of black bears in the Southern Appalachian region. Department Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville.

Johnson, K. G., editor. 1990. Annual progress report—1990: Bait-station surveys to determine relative density, distribution, and activities of black bears in the Southern Appalachian region. Department Forestry, Wildlife and Fisheries, University of Tennessee, Knoxville.

Johnson, K. G., and M. R. Pelton. 1980. Prebaiting and snaring techniques for black bears. Wildlife Society Bulletin **8:**46-54.

Jonkel, C. J., and I. McT. Cowan. 1971. The black bear in the spruce-fir forest. Wildlife Monographs **27:**1-57.

Kolenosky, G. B. 1990. Reproductive biology of black bears in east-central Ontario. International Conference of Bear Research and Management **8:**385-392.

LeCount, A. L. 1983. Evidence of wild black bears breeding while raising cubs. Journal of Wildlife Management **41:**408-412.

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

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika **33**:183-212.

Leslie, P. H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika **35**:213-245.

Pelton, M. R. 1982. Black bear (*Ursus americanus*). Pages 504-514 in J. A. Chapman, and G. A. Feldhamer, editors. Wild mammals of North America. The Johns Hopkins University Press, Baltimore.

Powell, R. A. 1987. Black bear, *Ursus americanus* Pallas. Pages 33-36 in M. K. Clark, editor. Endangered, threatened, and rare fauna of North Carolina. Part I. A re-evaluation of the mammals. Occasional paper 1987-3. North Carolina Biological Survey, Raleigh.

Powell, R. A., and D. E. Seaman. 1990. Production of important black bear foods in the Southern Appalachians. International Conference on Bear Research and Management **8**:183-187.

Powell, R. A., J. W. Zimmerman, and D. E. Seaman. 1992. Evaluation of a black bear sanctuary in the mountains of western North Carolina. Final report. Federal aid in wildlife restoration project W-57. Wildlife Management Division, North Carolina Wildlife Resources Commission, Raleigh.

Quigley, H. B. 1982. Activity patterns, movement ecology, and habitat utilization of black bears in the Great Smoky Mountains National Park, Tennessee. University of Tennessee, Knoxville.

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

Rogers, L. L. 1977. Social relationships, movements and population dynamics of black bears in northeastern Minnesota. Ph.D. dissertation. University of Minnesota, Minneapolis.

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

Sanders, O. T., K. Johnson, and J. Reiffenberger. 1978. An evaluation of black bear sanctuaries. Pages 278-297 in Proceedings of the Fourth Eastern Black Bear Workshop.

Servheen, C. 1989. The status and conservation of the bears of the world. International Conference on Bear Research and Management. Monograph Series **2**:1-32.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, England.

Warburton, G. S. 1984. An analysis of a black bear sanctuary in western North Carolina. M.S. thesis. North Carolina State University, Raleigh.

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

Zimmerman, J. W. 1992. A habitat suitability index model for black bears in the Southern Appalachian Region evaluated with the incorporation of location error. Ph.D. dissertation. North Carolina State University, Raleigh.

Zimmerman, J. W., and R. A. Powell. 1995. Radio telemetry error: location error method compared to error polygons and error ellipses. Canadian Journal of Zoology **73**:1123-1133.