

LONG-TERM ANALYSIS OF SURVIVAL, FERTILITY, AND POPULATION GROWTH RATE OF BLACK BEARS IN NORTH CAROLINA

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We estimated survival, fertility, and realized and asymptotic population growth rates from 1981 to 2002 for a protected population of black bears (*Ursus americanus*) in the southern Appalachian Mountains. We used Akaike's information criterion to assess the time interval for averaging observations that was best for estimating vital rates for our study, given our yearly sample sizes. The temporal symmetry approach allowed us to directly assess population growth and to address all losses and gains to the population by using only capture data, offering an alternative to the logistically intensive collection of reproductive data. Models that averaged survival and fertility across 5- and 7-year time intervals were best supported by our data. Studies of black bear populations with annual sample sizes similar to ours should be of at least 5 years in duration to estimate vital rates reliably, and at least 10 years in duration to evaluate changes in population growth rate (λ). We also hypothesized that survival would not track changes in λ because λ is influenced by both survival and fertility. The 5-year model supported our hypothesis, but the 7-year model did not. Where long-term dynamics of large, relatively stable bear populations are of interest, monitoring survival is likely to be sufficient for evaluating trends in λ . For rapidly changing, small populations, however, failure to incorporate fertility into assessments of λ could be misleading.

Key words: black bears, demographic analysis, fertility, North Carolina, population growth rate, program MARK, southern Appalachians, survival, temporal symmetry, *Ursus americanus*

Monitoring populations of terrestrial carnivores can be difficult because individuals often are long-lived, solitary, elusive, and have low reproductive rates (Schaller 1996). Bekoff et al. (1984) emphasized the need for long-term field projects that monitor life-history patterns of unexploited populations of carnivores to understand general carnivore ecology and to lay the necessary groundwork for theoretical questions. Nearly 20 years later, few such studies have been published, and fewer than 15% of terrestrial carnivores have been studied intensively (Schaller 1996). Understanding survival and fertility, and their combined effect on population growth rate (λ , the rate of population change—Ricklefs 1990), is a necessary 1st step in examining life-history patterns.

Our analysis examined the long-term (22-year) dynamics of the population of black bears in the Pisgah Bear Sanctuary of western North Carolina. Many studies of black bear population

dynamics span periods less than 5 years (Clark and Smith 1994; Doan-Crider and Hellgren 1996; Hellgren and Vaughan 1989; Lindzey and Meslow 1977; Samson and Hout 1995). Examining variation in survival at annual or shorter intervals is relatively easy for smaller and more abundant animals, but for large carnivores it is difficult to obtain enough observations to estimate annual vital rates. Because the number of males in a population of black bears does not limit the fertility of females (Schenk and Kovas 1995), growth of a black bear population is determined by the number of females and the number of cubs each female can produce. The majority of studies on black bear populations have sample sizes of <10 females per year. Consequently, estimates of vital rates for black bears often are averaged across years (Beringer et al. 1998; Eiler et al. 1989; Hellgren and Vaughan 1989; Kasbohm et al. 1996; Powell et al. 1996; Sorensen and Powell 1998). With typically small sample sizes, 2- and 3-year studies may be too short to obtain precise estimates with so few captured individuals. Although Pelton and van Manen (1996) did not estimate survival, fertility, or λ , they concluded that their estimates of population size when using a long-term (28-year) data set from the black bears in the Great Smoky Mountains

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National Park would have been interpreted much differently had the study been of shorter duration. Given the sample sizes typical for studies of large, solitary carnivores such as black bears, long-term studies clearly are necessary to understand population dynamics. What is not clear is how long a study must be to estimate vital rates and changes in population size precisely and accurately.

Accurate and precise estimation of demographic parameters depends in part on the methodology used. Other survival studies in the southeastern United States have used methods ranging from confirmed mortalities (Hellgren and Vaughan 1989) to Jolly-Seber (Clark and Smith 1994) and Kaplan-Meier estimators (Sorensen and Powell 1998). A small number of studies have used temporal symmetry to calculate recruitment rates and λ for insects and birds (Oro and Pradel 2000; Pradel 1996; Pradel et al. 1997; Sandercock and Beissinger 2002; Schaub et al. 1999). Our research is the 1st to use a temporal symmetry approach to estimate survival and fertility for a large mammal when using only capture-recapture data. This approach (Pradel 1996) allowed us to estimate survival, fertility, and population growth rate from mark-recapture data alone without the assumption of asymptotic growth. Asymptotic growth is only achieved when vital rates and population structure are static (Nichols and Hines 2002), which is not the case for survival and fertility of the bears in Pisgah (Powell et al. 1996, 1997; Sorensen and Powell 1998). The temporal symmetry approach eliminates the time-consuming and difficult task of locating dens of female bears or corpora lutea analysis to assess cub production. Also, because the temporal symmetry approach uses mark-recapture data instead of reproductive data to estimate vital rates, the population growth rate reflects all losses from and gains to the population, not just those from births and deaths (Nichols and Hines 2002).

Our objective was to estimate survival, fertility, and λ for the population of black bears in the Pisgah Bear Sanctuary, and to track the changes in those parameters over a 22-year period. Within that objective, we wanted to assess which time interval for averaging observations was best for estimating vital rates for our study, given our yearly sample sizes. Time intervals for vital rate estimates often are dictated by the length of a study. If research is conducted for 3 years, then vital rates are averaged over those 3 years; if 3 years of observations are required for precise estimates of vital rates, however, then an estimate of changes in vital rates or λ (which requires 2 sets of estimated vital rates) is not possible unless observations are collected over 6 years. Long-term research offers 2 opportunities unavailable in short-term studies: combining observations over longer time intervals for more precise estimates of vital rates, and estimating vital rates over multiple time intervals, allowing estimation of λ .

Vital rates estimated from small sample sizes (i.e., brief intervals) are likely to lack precision and could thus be uninformative or misleading. Use of large sample sizes from long-term studies without subdividing into smaller time intervals, on the other hand, will yield precise estimates but will gloss over potentially important short-term dynamics. A balance must be struck between increasing precision of estimates while still

capturing as many of the short-term dynamics as possible. We hypothesized that the best time intervals for estimation would be greater than the median time interval for estimation in survival studies of black bears in the Southeast (4 years—Beringer et al. 1998; Clark and Smith 1994; Hellgren and Vaughan 1989; Kasbohm et al. 1996; Sorensen and Powell 1998) but less than the entire duration of our study.

Sorensen and Powell (1998) estimated survival of the bears studied in the Pisgah Bear Sanctuary from 1981 to 1996. They found that implementation of law enforcement in 1988 led to reduced poaching and increased survival (Sorensen and Powell 1998). Sorensen and Powell (1998) addressed the effect of management actions on survival but did not address their effect on λ . Survival rates alone may not necessarily indicate the direction or magnitude of changes in population size because λ also depends on fertility. Thus, to better understand the dynamics of populations, estimates of both survival and fertility may be required. Powell et al. (1996) examined survival, fecundity, and asymptotic population growth rate (λ_a) for the Pisgah population from 1981 to 1990 but did not analyze changes over time. We hypothesized that survival followed the pattern found by Sorensen and Powell (1998) but that it would not track changes in λ because λ is influenced by both survival and fertility.

MATERIALS AND METHODS

Study area.—The Pisgah Bear Sanctuary is located in the southern Appalachian Mountains of North Carolina (35°17'N, 82°47'W, elevation 650–1,800 m). The 235-km² sanctuary is contained in the Pisgah National Forest, and the major road through the sanctuary is the Blue Ridge Parkway. Oak (*Quercus*), pine (*Pinus*), and pine-hardwood are the major forest types of the sanctuary. The forest understory is often dense with rhododendrons (*Rhododendron*), laurels (*Kalmia*), other ericaceous shrubs, and berry bushes (*Vaccinium*, *Gaylussacia*, and *Rubus*). The area is considered a temperate rainforest, with high (up to 250 cm/year) annual rainfall. Human use of the area includes hiking, biking, camping, and hunting for species other than bears (Powell et al. 1997).

Mark-recapture.—We livetrapped bears from May to July in 1981–2002 by using modified Aldrich foot snares (Johnson and Pelton 1980) or culvert traps. We used a blow dart or jab stick to administer either a 2:1 combination of ketamine hydrochloride and xylazine (10 mg/kg) or telazol (at 5 mg/kg estimated weight). We measured bears, drew blood, and extracted a premolar for age identification via cementum annuli (Willey 1974). We recorded body mass, sex, and body condition of each captured bear (Powell et al. 1997). Each bear received 2 ear tags and 2 tattoos with a unique number for identification upon recapture. Recaptured bears received new tags and tattoos if necessary. All bears were captured and handled in compliance with requirements of the Institutional Animal Care and Use Committees for North Carolina State University and Auburn University and with the guidelines recommended by the American Society of Mammalogists (Animal Care and Use Committee 1998).

Estimation of vital rates and λ .—In our analyses, we used only females. We assumed no emigration or immigration, because female black bears usually do not disperse (Elowe and Dodge 1989; Schwartz and Franzmann 1992).

Pradel's (1996) temporal symmetry approach used inverted capture histories to estimate seniority, the probability of previously being in

the population, and its complement, recruitment in the absence of actual reproduction data by estimating both annual survival rates (ϕ , the probability that an individual in the population at time t will be in the population at time $t + 1$) and annual fertility rates (f , i.e., female young recruited per female annually). For black bears, the recruitment rate estimated by Pradel's model must be adjusted because females do not reproduce until ≥ 3 years of age. Thus, we present estimates of female young produced per adult female per year (f_n). The temporal symmetry approach also allows for the estimation of the realized population growth rate (λ_r), which represents the observed change in a population size between 2 time units. λ_r differs from λ_n in that it does not assume constant exponential growth and stable age distribution as does λ_n .

We used program MARK (White and Burnham 1999) to analyze capture histories. We used the temporal symmetry survival and recruitment model (Pradel 1996) to estimate ϕ , f , and recapture probability (p). We evaluated 7 models that estimated the mean of ϕ and f over time intervals (2-, 3-, 4-, 5-, 7-, 10-, and 21-year time intervals) that were relatively equal over the duration of the study. For example, our 2-year model had 11 time intervals, each 2 years long. We constrained ϕ and f to be equal among years within time intervals, but allowed ϕ and f to vary among time intervals because we were interested in examining changes over time for those 2 parameters. Because we were not specifically interested in estimates of recapture rate (p), we allowed those estimates to vary annually (Cooch and White 2002). Forty-six percent of bears 1st captured as juveniles and 48% of bears 1st captured as adults were recaptured, so we assumed nondifferential recapture rates between juveniles and adults.

Clark and Smith (1994) and Sorensen and Powell (1998) found no differences among annual survival rates of different age classes of black bears. Lack of evidence for differential survival among ages may have been a product of small sample size in these cases. Estimation of age-specific survival is possible within the temporal symmetry framework if age classes are split into separate groups. However, information is lost when a bear is moved from one age group to another. When a bear turns 3 years of age it would be censored from the juvenile group and added to the adult group. Because the 2 groups are completely separate, the 1 bear in the 2 groups is considered as 2 individuals. Our annual sample sizes were similar to those of Clark and Smith (1994) and Sorensen and Powell (1998), which means we probably could not show differential juvenile and adult survival, so we chose to assume equal survival rates across juveniles and adults.

For each time interval, we estimated 1 fertility rate (f) for all age classes. Fertility is relatively uniform across ages once black bears reach sexual maturity (Clark and Smith 1994; Hellgren and Vaughan 1989). Because black bears in North Carolina do not reproduce until age 3 (Powell et al. 1997), we determined the age distribution for the population at each time group by calculating the ratio of juveniles (< 3 years old) to adults (≥ 3 years old) from all females captured. We then divided the original fertility estimate for that time interval by the proportion of the population that was adult to represent adult fertility (f_n). A goodness of fit test appropriate to the temporal symmetry approach is not available (Cooch and White 2002), so we used a bootstrap approach based on the Cormack–Jolly–Seber model to calculate \hat{c} (Franklin et al. 2004).

We ranked the models by using Akaike's information criterion adjusted for small sample uncertainty (AICc—Akaike 1973; Anderson et al. 1998). The highest-ranking model was the most parsimonious given the data, and subsequent models were ranked in relation to the most parsimonious model with Δ AICc. We normalized Δ AICc values into model weights (w), representing the probability that the given model is the most parsimonious given the suite of possible models. We

TABLE 1.—Rankings for models of survival (ϕ), fertility (f), and recapture rates (p) of black bears from 1981 to 2002 in the Pisgah Bear Sanctuary, North Carolina.

Model ^a	AICc ^b	Δ AICc	AICc weight	Parameters	Deviance
$\phi_7 f_7 p_t$	977.917	0.000	0.451	28	743.493
$\phi_5 f_5 p_t$	978.461	0.544	0.344	30	738.143
$\phi_4 f_4 p_t$	980.695	2.778	0.112	32	734.310
$\phi_t f_t p_t$	981.994	4.077	0.059	24	758.862
$\phi_{10} f_{10} p_t$	984.293	6.376	0.019	26	755.595
$\phi_3 f_3 p_t$	984.954	7.037	0.013	35	729.123
$\phi_2 f_2 p_t$	988.473	10.556	0.002	40	715.906

^a Numerical subscripts represent the number of years constrained to be equal for estimates of ϕ and f ; t indicates that estimates of p are completely time variant.

^b AICc = Akaike's information criterion adjusted for small sample uncertainty.

considered any model with a $w > 0.25$ and Δ AICc < 2.00 a good approximating model, and retained it for further analyses (Williams et al. 2002). We also used model-averaging in program MARK to obtain annual estimates of vital rates. The annual estimates are average estimates from all models weighted relative to their AICc ranking.

We calculated λ for those models with $w > 0.25$ and Δ AICc < 2.00 and for the lowest-ranking model, as well as the model-averaged estimates, to compare estimates from models that were good and poor estimators of the vital rates. We estimated λ_r directly as the sum of ϕ and f rates from each time period. The direct estimation of λ reflects the actual change in population size between 2 time periods. For comparison with λ_r , we also calculated an λ_n , which assumes asymptotic population growth and stable age distribution, as the dominant eigenvalue of the pseudo age-structured projection matrix (Lefkovich 1965) constructed from the estimated survival and fertility rates. λ_n represents the growth that would be achieved if vital rates remain constant. To estimate variance on λ_n , we also calculated mean λ_n from each of the best time intervals for estimation and constructed 95% confidence limits on mean λ_n by using a Monte Carlo resampling procedure (Caswell et al. 1998). We constructed 10 matrices by using vital rates from shorter time periods within the best time intervals for estimation and used those 10 matrices as resampling units for the Monte Carlo procedure. We used 1,000 iterations for each best time interval for estimation, then took the mean and 95% confidence limit from those 1,000 iterations.

RESULTS

We captured 101 females 194 times from 1981 to 2002. The average number of females captured per year was 8.82 ± 4.33 SD. Two models of survival and fertility fit the data well. The model with vital rates grouped in 7-year increments was the best approximating model, followed by the model with vital rates grouped in 5-year increments (Table 1). These 2 models together accounted for 79.5% of the model weights, suggesting a high probability that these are the best models given the data and the suite of models. The estimate of \hat{c} calculated with the Cormack–Jolly–Seber model was 1.3, which when adjusted did not change the rankings of the models. Average recapture rates over all years for the 7- and 5-year models were 38% and 37%, respectively.

Survival and fertility rates in the 7-year model ranged from 0.592 ± 0.067 to 0.827 ± 0.054 and 0.419 ± 0.109 to 0.692 ± 0.128 , respectively, and asymptotic λ from the

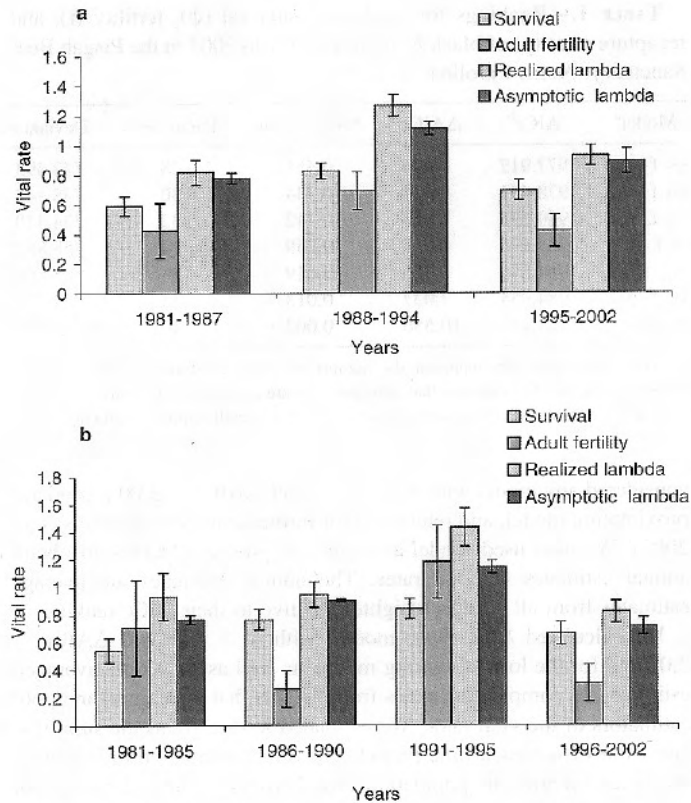


FIG. 1.—Estimates of survival, adult fertility, realized population growth rate, and asymptotic population growth rate for a) 7-year time periods and b) 5-year time periods for the population of black bears in the Pisgah Bear Sanctuary, North Carolina, from 1981 to 2002, shown as mean \pm SE.

population projection ranged from 0.801 ± 0.035 to 1.022 ± 0.042 (mean \pm SE; Fig. 1a). Trends for both survival and fertility were low at the beginning of the study, increased in the middle years, and decreased again near the end of the study. Estimates of survival differed (SEs did not overlap) across all three 7-year periods (Fig. 1a). Fertility showed similar trends, although the increase in the middle time period was not significant (SEs overlapped). However, the increase in fertility between the 2nd and 3rd time periods was significant (Fig. 1a). Estimates of survival and fertility in the 5-year model were more variable than those of the 7-year model, and patterns in survival and fertility did not associate as closely as they did in the 7-year model. Fertility was relatively low and did not differ between the first and fourth 5-year period, was moderate in the 1st period, and was high in the 3rd; survival was relatively low in the 1st period, was moderate and did not differ between the 2nd and 3rd periods, and was lower again in the 4th period (Fig. 1b).

Survival estimates from the 5- and 7-year models were comparable. Fertility estimates of the 7- and 5-year models were comparable except for the late 1980s, when the 5-year model indicated a decrease in fertility but the 7-year model did not (Fig. 1). Patterns in the annual model-averaged estimates of vital rates were similar to the 7- and 5-year models (Fig. 2). Because model-averaging incorporates model weights, the

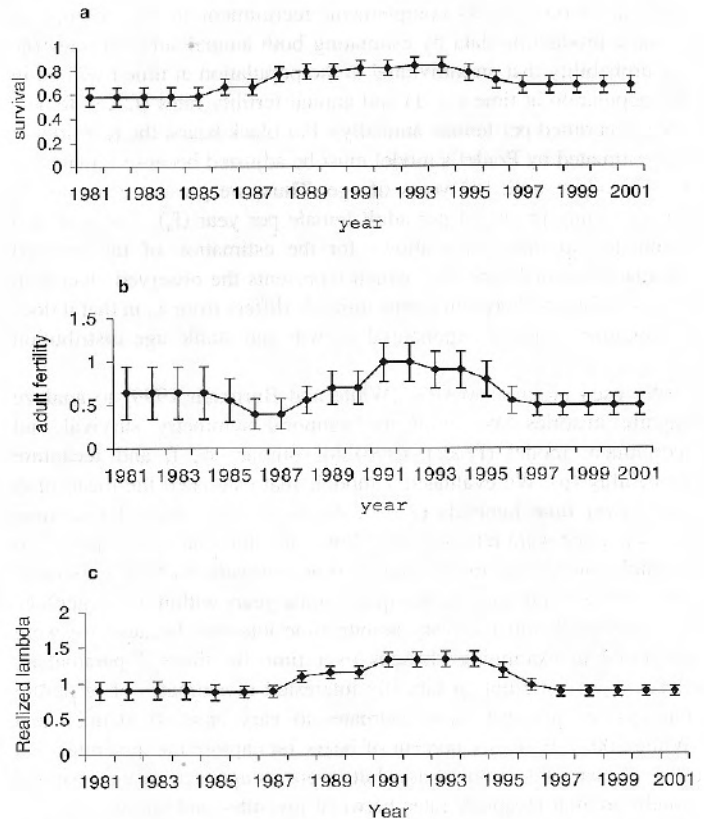


FIG. 2.—Estimates of a) survival, b) fertility, and c) realized population growth rate, calculated as the weighted average of all models, with SE bars, for the population of black bears in the Pisgah Bear Sanctuary, North Carolina, from 1981 to 2002.

model-averaged estimates for fertility reflected a decrease in fertility in the late 1980s, but the greater weight of the 7-year model reduced the severity of the decrease seen in the 5-year model.

Asymptotic and realized estimates of λ were never identical, but they were at least similar. For each time grouping in the 5- and 7-year models, λ_r was greater than λ_a (Fig. 1). Both estimates followed a similar trend over all time intervals (Fig. 1). In the 7-year model, both estimates of λ showed that the population was decreasing in the early 1980s, increasing in the late 1980s and early 1990s, then decreasing again in the late 1990s through 2002 (Fig. 1a). Survival estimates closely tracked estimates of λ in the 7-year model. The 5-year model showed a similar but statistically different pattern (Fig. 1b). Survival was moderate in the first 5-year period, was high and did not differ in the 2nd and 3rd periods, and was low in the last period, whereas λ was moderate and did not differ between the first 2 periods, was high in the 3rd, and was low in the last period.

DISCUSSION

The 7- and 5-year time intervals for estimation of vital rates were best supported by our data. Given our annual sample sizes, the small numbers of recaptures each year provide little confidence in estimates of vital rates from models

that estimate over shorter time periods. Models with time intervals greater than 7 years, on the other hand, were precise but they smoothed over much of the yearly variation in the dynamics of the population. Our time intervals are not directly applicable to all bear studies because best-estimating time intervals are influenced by sample size. Bear studies with annual sample sizes similar to ours (which includes all other published studies of bears in the southeastern United States [Clark and Smith 1994; Hellgren and Vaughan 1989; Kasbohm et al. 1996; Sorensen and Powell 1998]) most likely need to average observations over 5- to 7-year intervals before reliable demographic trends can be estimated. Studies with significantly greater sample sizes than ours likely would be able to estimate vital rates over shorter time intervals. Given that best-estimating time intervals are dependent on sample size and recapture rates, we recommend that each study evaluate independently the best time interval for estimating vital rates.

Our highest-ranking model did not support our hypothesis that examining survival alone does not explain overall changes in population growth for black bears in Pisgah. In the 7-year model, λ corresponded closely to annual survival. However, the 5-year model illustrates how assuming population trends from survival can gloss over important details and potentially be misleading. The 5-year model reveals patterns not evident from the 7-year model, including a decoupling of estimates for survival and λ , as well as strong changes in fertility that appear to have affected λ . The combined effect of the increase in survival and the decrease in fertility in the late 1980s caused λ to remain relatively constant. We hypothesize that monitoring survival may be sufficient for tracking changes for a relatively large, stable population of black bears such as the one in Pisgah. For small or rapidly changing populations of black bears, we hypothesize that estimates of both survival and fertility are required for estimating changes in population growth accurately.

Our estimates of survival from the early to mid 1980s (0.58–0.66) generated through model-averaging were similar to, although slightly higher than, those of Sorensen and Powell (1998—0.48 from 1981 to 1987). Our estimates of survival, as well as those of Sorensen and Powell (1998), increased in the late 1980s and early 1990s. Sorensen and Powell's (1998) estimate of survival of females (0.97) from 1988 to 1996 was higher than our estimates (0.77–0.84). The time intervals used by Sorensen and Powell (1998) were similar to our best-estimating time intervals, but annual sample sizes afforded by their Kaplan–Meier approach were smaller than our annual sample sizes. Assuming a 1:1 sex ratio in the radiocollared bears they analyzed, Sorensen and Powell (1998) monitored 6.1 (± 3.27 SD) radiocollared females per year. This small sample size may provide reliable estimates for the collared individuals, but could lead to biased estimates when extrapolating to the entire population. Sorensen and Powell (1998) concluded that the changes they found in survival may be related to the high incidence of poaching in the early 1980s, which dropped off in the late 1980s and early 1990s after significant law enforcement activities. Our estimates of survival correlate with Sorensen and Powell's (1998) estimates,

although our more moderate results suggest that the influence of poaching on survival may not have been as great as originally thought.

Three other survival studies have been performed on black bears in the southeastern United States (Clark and Smith 1994; Hellgren and Vaughan 1989; Kasbohm et al. 1996). All of these produced survival rates of females higher than ours (0.83–0.95, 0.84–0.95, and 0.88–0.90, respectively). The discrepancy in survival rates is not likely due to poor survival in Pisgah because the population is protected and the habitat is of high quality (Mitchell et al. 2002). One possible explanation is that the median time interval for estimation of these 3 studies was 3 years and sample sizes were comparable to ours. Another explanation could be a violation of our assumption that there was no immigration or emigration during our study. Although we deem it unlikely, female bears emigrating from the sanctuary could bias our survival estimates negatively.

To our knowledge, this is the 1st attempt to estimate fertility of black bears by using methods other than direct measurement of cub production. Fertility estimation from capture data could be very valuable to studies that cannot afford the extensive time and resources involved in den searches or corpora lutea analysis. Further, although our estimates are not separable into cub production and proportion of reproducing adults, a reliable measure of females per adult female per year is a valuable estimate for tracking general changes in recruitment over time. Our fertility estimates, which incorporate survival to capture season, are less than the fecundity estimates of Powell et al. (1996). This is expected because fecundity estimates of Powell et al. (1996) do not incorporate survival to capture season, and cubs often do not survive the period from birth until capture season.

Our top-ranking models, as well as our model-averaged estimates of vital rates, indicated that the bear population in Pisgah was declining ($\lambda < 1.0$) in the early to mid-1980s, then began increasing ($\lambda > 1.0$) after 1988. This change corresponds to the increased law enforcement against poaching. Estimates of λ from the mid-1990s through 2002 indicated that the population was once again decreasing. Future research should explore possible factors in that decrease, such as a resurgence in poaching, changes in habitat, or potential density-dependent mechanisms.

The time intervals over which we averaged vital rates were arbitrary; grouping years together allowed us to bolster sample size and increase the precision of vital rate estimates. As a result, our models likely are overparameterized, and our estimates may be somewhat biased. Despite this grouping of observations by arbitrary time intervals, model-averaged estimates provided insights into annual variation and long-term patterns in vital rates because they incorporated the information from all models. Future research that seeks to avoid arbitrary time groupings could develop models based on biologically relevant time intervals, such as changes in environmental factors that covary with vital rates. For example, if vital rates are found to covary with annual food productivity, then time intervals for vital rate estimation could correspond to cycles in food production.

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