Contributions of vital rates to growth of a protected population of American black bears

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Abstract: Analyses of large, long-lived animals suggest that adult survival generally has the potential to contribute more than reproduction to population growth rate (λ), but because survival varies little, high variability in reproduction can have a greater influence. This pattern has been documented for several species of large mammals, but few studies have evaluated such contributions of vital rates to λ for American black bears (*Ursus americanus*). We used variance-based perturbation analyses (life table response experiments, LTRE) and analytical sensitivity and elasticity analyses to examine the actual and potential contributions of variation of vital rates to variation in growth rate (λ) of a population of black bears inhabiting the Pisgah Bear Sanctuary in the southern Appalachian Mountains of North Carolina, using a 22-year dataset. We found that recruitment varied more than other vital rates; LTRE analyses conducted over several time intervals thus indicated that recruitment generally contributed at least as much as juvenile and adult survival to observed variation in λ, even though the latter 2 vital rates had the greater potential to affect λ. Our findings are consistent with predictions from studies on polar bears (*U. maritimus*) and grizzly bears (*U. arctos*), but contrast with the few existing studies on black bears in ways that suggest levels of protection from human-caused mortality might explain whether adult survival or recruitment contribute most to variation in λ for this species. We hypothesize that λ is most strongly influenced by recruitment in protected populations where adult survival is relatively high and constant, whereas adult survival will most influence λ for unprotected populations.

Key words: American black bear, elasticity, life table response experiments, North Carolina, population growth rate, population modeling, sensitivity, Southern Appalachians, *Ursus americanus*, vital rates

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Analytical sensitivity and elasticity analyses quantify the potential for infinitesimal changes in vital rates to affect annual population growth rate (λ), given equal absolute (sensitivity) or proportional (elasticity; de Kroon et al. 2000) changes for each vital rate (Horvitz et al. 1997). In contrast, variance-based sensitivity analyses (such as life table response experiments, LTRE, or life-stage simulation analyses, LSA) incorporate variation in vital rates, as well as the infinitesimal effects of those rates, to estimate the overall contribution of vital rates to actual changes in λ (Horvitz et al. 1997, Wisdom et al. 2000, Mills and Lindberg 2002, Mills 2007). Analytical sensitivity and elasticity analyses deal only with equal, infinitesimal changes in λ; because variance-based analyses incorporate the extent to which vital rates change in nature or under management, the 2 approaches can yield different results (Mills et al. 1999, Hoekman 2002, Mills 2007).

'Slow' mammals on the 'slow–fast' continuum (Romanovsky 2002) mature late, have few offspring, have high adult survival, and generally have high survival elasticities (Heppell et al. 2000). For such animals, however, survival may vary little because natural selection minimizes the variation of the demographic parameter to which λ is most sensitive (Pfister 1998, Gaillard et al. 2000). Lack of variation in the vital rate to which λ is most sensitive, causing

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Table 1. Estimates of apparent survival (ϕ), adult recruitment (f_a), and asymptotic population growth rate (λ) from the 7- and 5-year grouping models for the population of black bears in the Pisgah Bear Sanctuary, North Carolina, USA from 1981–2002 (Brongo et al. 2005).

Intervals	ϕ	SE	f_a	SE	λ
7-year intervals					
1981–87	0.592	0.067	0.425	0.186	0.779
1988–94	0.827	0.054	0.692	0.128	1.112
1995–2002	0.695	0.069	0.419	0.109	0.893
5-year intervals					
1981–85	0.546	0.091	0.709	0.334	0.785
1986–90	0.766	0.074	0.264	0.133	0.919
1991–95	0.843	0.073	1.180	0.264	1.226
1996–2002	0.664	0.081	0.303	0.134	0.823

greater actual contributions of vital rates to which λ is less sensitive, has been shown in populations of birds (Cooch et al. 2001), small mammals (Oli et al. 2001), and ungulates (Gaillard et al. 1998, Raithel et al. 2007).

High survival with highly variable reproduction has been shown for grizzly bears (*Ursus arctos*; McLoughlin et al. 2003, Garshelis et al. 2005, Harris et al. 2006). Population models for grizzly bears (Wielgus et al. 2001, Garshelis et al. 2005, Harris et al. 2006, Kovach et al. 2006) and polar bears (*U. maritimus*; Taylor et al. 1987, Eberhardt 1990) showed λ was most sensitive to adult survival. Garshelis et al. (2005) and Harris et al. (2006) showed, however, that variation in reproduction made greater contributions to variation in λ for grizzlies even though adult survival had the highest elasticity. Ecological similarities among bears (generation time, age at maturity, adult survival; Heppell et al. 2000) suggest American black bears (*U. americanus*) should show a similar pattern. Survival rates published for black bears are typically high (Hellgren and Vaughn 1989, Clark and Smith 1994, Kasbohm et al. 1996; but see Powell et al. 1996) but much less variable than published reproductive rates (Clark and Smith 1994, Kasbohm et al. 1996). Few analyses of vital rate contributions to variation in λ, however, have been performed on black bears. Powell et al. (1996) used analytical sensitivity and elasticity analyses to show that both sensitivity and elasticity were highest for survival of cubs, 1-year olds, and 2-year olds for a population in western North Carolina, USA. Hebblewhite et al. (2002) also used analytical sensitivity analysis to show that λ was most sensitive to infinitesimal changes in survival of adult females for a population of black bears near Banff National Park, Canada. In a broad analysis of black bear populations inhabiting the Southeastern Coastal Plain of the US, Freedman et al. (2003) used LSA to show adult survival and litter size of 3- to 4-year-old females made the greatest contributions to variation in λ. The paucity of studies, combined with variation in their inferences, suggests more research is needed to understand how vital rates contribute to variation in λ for black bears.

Our objective was to evaluate how vital rates influence variation in λ for a population of black bears inhabiting the Pisgah Bear Sanctuary (where bear hunting is illegal), in the Southern Appalachians of North Carolina, USA. This population was studied intensively for 22-years (1981–2002); data through 1990 were used by Powell et al. (1996) to construct their population models. Analyses of the complete data set showed that variability in vital rates of black bears in Pisgah is best estimated in 5- and 7-year intervals (Brongo et al. 2005).

Both apparent survival (the probability that an individual in the population at time t will be in the population at time $t + 1$) and recruitment (the number of female young produced per female of reproductive age that survive to capture season per year) varied considerably during the 22 years (Table 1). Both the 5- and 7-year models showed that the population decreased through the mid-1980s, increased in the late 1980s to mid 1990s, then decreased again from the late 1990s through 2002 (Table 2). These changes in λ offered an opportunity to evaluate the extent to which different vital rates contributed to population growth over a long time. Thus, we used LTRE analysis and analytical sensitivity and elasticity analyses (Caswell 2001) to examine how variation in different vital rates contributed to changes in the population growth of black bears in Pisgah. We assessed the vital rates of 2 portions of the population, juveniles and adults, which function separately to influence λ. We used results of our analyses to test 2 hypotheses:

Table 2. Mean population growth rates (λ) with 95% confidence limits from Monte Carlo resampling analysis of vital rates estimated in 7- and 5-year intervals for the population of American black bears in the Pisgah Bear Sanctuary, North Carolina, USA, 1981–2002 (Brongo et al. 2005).

Intervals	λ	Lower 95% CL	Upper 95% CL
7-year intervals			
1981–87	0.801	0.736	0.873
1988–94	1.110	1.022	1.196
1995–2002	0.829	0.665	0.996
5-year intervals			
1981–85	0.768	0.707	0.832
1986–90	0.902	0.882	0.924
1991–95	1.143	1.053	1.235
1996–2002	0.716	0.593	0.834

1. Due to high selection pressure on survival, especially adult survival, sensitivity and elasticity of adult survival would be greater than sensitivity and elasticity of juvenile survival or adult recruitment.
2. Greater variation in recruitment than in juvenile or adult survival would result in greater actual contributions of recruitment to observed changes in λ than those of juvenile or adult survival.

Study area

The Pisgah Bear Sanctuary is located in the Southern Blue Ridge Mountains within the Southern Appalachians (35°17′N, 82°47′W). The 235-km^2 sanctuary is in the Pisgah National Forest, and The Blue Ridge Parkway runs through the northern end of the sanctuary. Elevation in the sanctuary ranges from 650 m to almost 1800 m. Oak (*Quercus* spp.), pine (*Pinus* spp.), and pine–hardwood are the major forest types in the sanctuary. The forest understory was often dense with rhododendrons (*Rhododendron* spp.), ericaceous shrubs, and berry bushes (*Vaccinium* spp., *Gaylussacia* spp., and *Rubus* spp.). Annual rainfall was 250 cm. Human use of the area included hiking, biking, camping, hunting (not of bears), and other recreation (Powell et al. 1997).

Methods

Vital rate estimation

For our analyses, we used data on 101 females captured 194 times from 1981 to 2002 in the Pisgah Bear Sanctuary (see Brongo et al. 2005 for details and methods used). We used the temporal symmetry described by Pradel (1996) to calculate survival and recruitment using inverted capture histories (Brongo et al. 2005). Reproductive rates calculated with the temporal symmetry approach use only capture–recapture data and are not composite estimates of lower-level rates such as natality and cub survival. Instead, this approach estimates seniority, the probability of previously being in the population, and its compliment, recruitment (annual female young recruited per adult female). For black bears, the recruitment rate estimated by Pradel's model must be adjusted because females reproduce every other year. Thus, we used estimates of female young produced per adult female each year (for example, 2 female young in a litter represent 1 female young per adult female per year).

Brongo et al. (2005) used Program MARK (White and Burnham 1999) to analyze capture histories and the temporal symmetry survival and recruitment model (Pradel 1996) to estimate apparent survival (probability that the animal is alive and remains on the study area, and hence is available for recapture, ϕ), recruitment (females produced per female that survive to be old enough to be captured, f_a), and recapture probability (p). Assuming geographic closure allowed Brongo et al. (2005) to ignore contributions of emigration to population growth; ϕ was an estimate of survival (probability the animal is alive) only. They compared models that estimated the mean ϕ and f_a over 7 different intervals (time intervals of 2, 3, 4, 5, 7, 10, and 21 years, within which numbers of captured bears were approximately equally distributed) over the duration of the study, and found that models that averaged survival rates over 5- and 7- year intervals were the best approximating models. Thus, we based our analysis on 7 parameterizations (3 using 7-year period estimates of vital rates, 4 using 5-year period estimates; Table 1) of a 4-stage birth-pulse, pre-breeding Lefkovitch matrix (Caswell 2001). For example, the matrix for the 7-year interval from 1981 to 1987 (Table 1) was:

$$\begin{bmatrix} 0 & 0 & 0 & 0.4250 \\ 0.5920 & 0 & 0 & 0 \\ 0 & 0.5920 & 0 & 0 \\ 0 & 0 & 0.5920 & 0.5920 \end{bmatrix}$$

To estimate variance of λ, we calculated mean asymptotic population growth rate (λ_a) from each of the best intervals for estimation and constructed 95% confidence limits for mean λ_a using a Monte Carlo resampling procedure (Caswell 2001).

We calculated the contribution of changes in each vital rate to changes in λ (dominant eigenvalue) over the study for the 5- and 7-year models following Caswell (2001) by first calculating the covariance among the matrix elements across periods and taking the product of the covariances and the matrix of sensitivities and its transpose. The matrix of covariances (C) is:

$$\mathbf{C} = E\left(\mathrm{vec}(\mathbf{A})\mathrm{vec}(\mathbf{A})^{\mathrm{T}}\right) - \mathrm{vec}(\mathbf{A})\mathrm{vec}(\mathbf{A})^{\mathrm{T}}$$

where **A** is the matrix model and **A** is the mean matrix; and the matrix of contributions (**V**) is:

$$\mathbf{V} = \mathbf{C}\left(\mathrm{vec}(\mathbf{S})\mathrm{vec}(\mathbf{S})^{\mathrm{T}}\right)$$

where **S** is the matrix of the sensitivities of each element of the matrix **A** (a_{ij}); and the elements of **S** (s_{ij}) are computed as:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}}$$

We calculated the relative contributions of each element by summing the columns of V and scaling them to sum to 1. The relative contribution represents the proportion of the total change in λ for which the respective vital rate was responsible (Caswell 2001).

We also calculated the elasticity (e_{ij}) of λ to each parameter of the Leslie matrix as:

$$e_{ij} = \left(\frac{\partial \lambda}{\partial a_{ij}}\right)\left(\frac{a_{ij}}{\lambda}\right)$$

(Caswell 2001). Because the first 3 stages of the matrix represent juveniles and the fourth stage represents all adults, contribution, sensitivity, and elasticity to juvenile survival is the sum of these properties across the first 3 stages of the model. Although survival is assumed to be equal for all ages, sensitivity and elasticity could differ for juvenile and adult survival because they take into account age structure and reproductive value, which is not equal for all ages.

Results

Sensitivity and elasticity of λ to both juvenile and adult survival were higher than to recruitment in both the 5- and 7-year groupings. In 2 of three 7-year groupings and 2 of four 5-year groupings, sensitivity and elasticity to adult survival were higher than to juvenile survival (Table 3). Contributions estimated from the 7-year model were $\phi_j = 0.382$, $\phi_a = 0.401$, and $f_a = 0.218$, whereas contributions estimated from the 5-year model were $\phi_j = 0.336$, $\phi_a = 0.318$, and $f_a = 0.346$ (Table 3). Recruitment varied most among vital rates (Table 3), thus its contribution to the variation in λ was similar to that of survival of adults and juveniles despite their greater degrees of sensitivity.

Discussion

Contrary to our first hypothesis, we cannot conclude that λ is more sensitive or elastic to changes in adult survival than to changes in juvenile survival. Consistent with our hypothesis, however, we can conclude that λ was more sensitive and elastic to changes in survival than to changes in recruitment. The relative potential of total survival to influence changes in λ was always several times that of recruitment in both the 5-year and 7-year groupings. Survival often varied little compared to recruitment (e.g., between the second and third, and third and fourth periods of the 5-year model; Table 1); therefore, the potential for survival to cause variation in λ suggested by its elasticity was often not realized.

In accordance with our second hypothesis, LTRE analysis of vital rates estimated over 5-year periods showed the actual contribution of recruitment to variation in λ was slightly higher than contributions of variations in adult or juvenile survival. By contrast, LTRE analysis of vital rates estimated over 7-year periods suggested stronger contributions of variation in juvenile and adult survival. We hypothesize 2 possible explanations for this contrast. First, grouping data over 7-year intervals instead of 5-years resulted in lower estimates of variability for recruitment (Table 1), suggesting the 7-year model could gloss over important annual variation in recruitment. If this were true, the importance of variation in recruitment to cause changes in λ would be underestimated by the 7-year model. Alternatively, the 7-year model may accurately partition important variability in adult survival because poaching of bears within the Pisgah Bear Sanctuary was sharply decreased by law enforcement in 1988 (Sorensen and Powell 1998), coinciding with the break between first and second 7-year groupings.

Table 3. Estimates of analytical sensitivity and elasticity of λ to juvenile survival (ϕ_j), adult survival (ϕ_a), adult recruitment (f_a), and variance-based estimates of overall contributions of ϕ_j, ϕ_a, and f_a to λ (Horvitz et al. 1997; Mills and Lindberg 2002) from models grouping data into 7- and 5-year intervals for a population of black bears in the Pisgah Bear Sanctuary, North Carolina, USA, from 1981–2002.

	Sensitivity			Elasticity		
Intervals	ϕ_j	ϕ_a	f_a	ϕ_j	ϕ_a	f_a
7-year intervals						
1981–87	0.550	0.582	0.256	0.418	0.442	0.139
1988–94	0.584	0.565	0.233	0.435	0.421	0.145
1995–2002	0.513	0.601	0.284	0.399	0.468	0.133
Overall contribution	0.382	0.401	0.218			
5-year intervals						
1981–85	0.686	0.523	0.176	0.477	0.364	0.159
1986–90	0.399	0.667	0.386	0.333	0.556	0.111
1991–95	0.704	0.516	0.168	0.484	0.355	0.161
1996–2002	0.455	0.633	0.332	0.367	0.511	0.122
Overall contribution	0.336	0.318	0.346			

Thus, adult survival could have varied enough between 1981–87 and 1988–94 that its potential contribution to variation in λ suggested by its elasticity could have been realized.

Our analytical sensitivity and elasticity analyses and LTRE analysis together indicate that vital rates varied in their contribution to population fluctuations of Pisgah bears over the 22 years we observed them. Whereas variation in survival had the greatest potential to influence λ, it generally varied little and thus did not consistently contribute strongly to changes in λ. Recruitment, regardless of its low potential, had a greater range of variability than survival and therefore contributed more to variation in λ than would be predicted based on its potential. Our understanding of the potential and actual contributions of vital rates depended somewhat on the length of time intervals used for grouping field data to estimate vital rates. The 5- and 7-year time intervals we used were determined by those found by Brongo et al. (2005) to produce the most reliable estimates of vital rates given the trapping effort and capture success of the Pisgah study. Grouping data over intervals $\geq$7 years has the potential to obscure important annual variation in vital rates. Had we used shorter time intervals, on the other hand, estimates of vital rates and their influence on λ would have been imprecise and thus uninformative (Brongo et al. 2005).

The accuracy of our analyses relies on 3 assumptions: (1) our estimates of the vital rates were accurate, (2) the Pisgah population exhibited asymptotic growth and was at a stable age distribution within each of the periods, and (3) that survival and recruitment of all females $\geq$3 years old was constant. Our estimates of vital rates were likely robust, calculated from a 22-year dataset divided into intervals shown to yield the most reliable estimates (Brongo et al. 2005). We have no reason to believe the assumption of asymptotic growth was violated within intervals for the Pisgah population. The asymptotic stable age distribution estimated from matrix models for our 5- and 7-year intervals suggested adults represented between 45 and 60% of the population, respectively; this closely approximates the 50 to 65% of adults in our capture data (Brongo 2003), suggesting the Pisgah bear population was close to a stable age distribution over the course of our study. Because previous research has not shown important differences in reproduction or survival among individual adult female black bears (Hellgren and Vaughn 1989, Clark and Smith 1994, Sorensen and Powell 1998), we deem it unlikely our assumption of constant survival and recruitment rates among adult female bears was violated.

Our results contrast in interesting ways with previous work. Contrary to our findings, and using some of the same data we used, Powell et al. (1996) reported highest sensitivity and elasticity to survival of the youngest 3 age classes. Freedman et al. (2003) suggested estimates of Powell et al. (1996) may be biased because they included both males and females in vital rate estimates, whereas female-only models would have been more appropriate (Yodzis and Kolenosky 1986). Alternatively, differences between our findings and those of Powell et al. (1996) could be their use of a collapsed Leslie (1948) matrix with 4 age classes for adults with sensitivities and elasticities calculated for each. Compared to the stage-based models that we, Hebblewhite et al. (2002), and Freedman et al. (2003) used, the age-based model used by Powell et al. (1996) partitioned contributions of vital rates of adult bears among age classes, resulting in relatively greater potential contributions of cubs and juveniles to changes in λ. Summing calculated elasticities across adult age classes used by Powell et al. (1996) results in elasticity for adult survival greater than those for the first 3 age classes (RAP, unpublished data).

In agreement with our findings, Hebblewhite et al. (2002) found that λ for a population of black bears inhabiting Banff National Park was most sensitive to changes in survival of adult females, but did not perform a variance-based analysis to which we can compare our results. The LSA approach used by Freedman et al. (2003) often yields estimates of vital rate contributions qualitatively comparable to LTRE analyses because they both take into account variation within vital rates (Wisdom et al. 2000, Mills and Lindberg 2002). It is noteworthy, therefore, that Freedman et al. (2003) found variation in survival of adults was the primary cause of variation in λ for bears living on the Southeastern Coastal Plain of the United States, not recruitment as we found. We hypothesize that the patterns in vital rates contributions to variation in λ across these studies and ours may be best explained by environmental variation across the modeled populations, which can cause vital rates contributions to vary considerably (Heppell et al. 2000). Specifically, we hypothesize variation in protection from human-caused mortality was the source of variation in vital rate contributions, where bears in the relatively protected Pisgah Bear Sanctuary and Banff National Park likely had relatively invariant levels of human-caused mortality than those occupying relatively unprotected lands on the Southeastern Coastal Plain (SCP). Differences in protection from human-caused mortality across these 3 study areas would be relative, requiring only that bears on the SCP had greater variation in human-caused mortality than bears in the other 2 locations. If our hypothesis is correct, survival would generally be higher and less variable in Pisgah and Banff than on the SCP, allowing greater contributions of recruitment to λ.

Management implications

Management strategies that target a vital rate with a low elasticity but high variance could have a greater impact on a population than targeting a vital rate with high elasticity but low variability (Mills et al. 1999, Wisdom et al. 2000). Our results suggest a moderate change in survival or a large change in recruitment could have similar effects on population growth in the Pisgah Bear Sanctuary, where bears are not legally hunted. Moderate changes to this level of protection (e.g., reducing road kills, allowing limited hunting) would have the greatest influence on population growth. Where level of protection is uniform and adult survival relatively constant, managing population growth is likely limited to broad-scale, long-term management of food productivity on the landscape, such as managing forest stands for production of hard and soft mast (Elowe and Dodge 1989, Reynolds-Hogland and Mitchell 2006, Reynolds-Hogland et al. 2007). For harvested populations, managers may need to understand both potential and actual contributions of vital rates to λ and how their importance can change over time, because sustainable harvests are difficult to achieve in places such as the Southeastern Coastal Plain where high-elasticity vital rates make strong contributions to variation in λ (Zuidema et al. 2007).

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