# Study design and sampling intensity for demographic analyses of bear populations

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***Abstract:*** The rate of population change through time (λ) is a fundamental element of a wildlife population's conservation status, yet estimating it with acceptable precision for bears is difficult. For studies that follow known (usually marked) bears, λ can be estimated during some defined time by applying either life-table or matrix projection methods to estimates of individual vital rates. Usually however, confidence intervals surrounding the estimate are broader than one would like. Using an estimator suggested by Doak et al. (2005), we explored the precision to be expected in λ from demographic analyses of typical grizzly (*Ursus arctos*) and American black (*U. americanus*) bear data sets. We also evaluated some trade-offs among vital rates in sampling strategies. Confidence intervals around λ were more sensitive to adding to the duration of a short (e.g., 3 yrs) than a long (e.g., 10 yrs) study, and more sensitive to adding additional bears to studies with small (e.g., 10 adult females/yr) than large (e.g., 30 adult females/yr) sample sizes. Confidence intervals of λ projected using process-only variance of vital rates were only slightly smaller than those projected using total variances of vital rates. Under sampling constraints typical of most bear studies, it may be more efficient to invest additional resources into monitoring recruitment and juvenile survival rates of females already a part of the study, than to simply increase the sample size of study females.

***Key words:*** American black bear, demographic analysis, grizzly bear, lambda, rate of increase, sample size, *Ursus americanus*, *Ursus arctos*, variability

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Knowing the trend of a population through time is generally thought of as fundamental to wildlife management, yet the difficulty of doing so in a rigorous manner means that it is rarely accomplished. This is particularly true for bears, whose naturally low densities and long life spans add to the challenges of obtaining precise estimates already presented by their life-histories.

For bears, 3 approaches have been used to estimate the population trend (λ) over some defined period (McDonald and Fuller 2001): (1) demographic analyses, which apply data on survival and reproductive rates of females captured and monitored for research to standard models of age-structured population growth (e.g., Eberhardt et al. 1994, Hovey and McLellan 1996) (2) mark–recapture modeling using either animals physically captured or identified through their DNA obtained from hair follicles (e.g., Brongo et al. 2005, Clark and Eastridge 2006, Clark et al. 2010), and (3) ratios of annual counts of females observed in the field who are identified through a rigorous procedure as being unique individuals (Knight et al. 1995, Brodie and Gibeau 2007, Cherry et al. 2007, Schwartz et al. 2008). Valuable as it is, we do not address the third approach in this paper.

Because the first 2 approaches rely on different data sources (radiomarked animals in the first, captures or DNA in the second) and thus require separate field protocols, the important conceptual difference between the 2 is sometimes under-appreciated. An estimate of λ obtained through a demographic analysis is an asymptotic value: It tells us the tendency of the population by integrating the myriad environmental and physiological factors affecting individuals via age-specific vital rates

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(termed 'demographic vigour' by Caughley 1977). But this does not necessarily correspond with the actual growth rate of the population during the period. Age-structure effects, sample biases, as well as undetected immigration and emigration (if the population is not geographically closed) can lead to divergence between the growth rate suggested by even the most rigorous demographic estimate of λ developed through projection methods and what actually transpired.

In contrast, mark–recapture approaches (e.g., Pradel model, Clark and Eastridge 2006, Stetz et al. 2010) estimate the actual growth rate of the population during the study period. In another example, Clark et al. (2010) used mark–recapture models based on both physical recaptures of bears as well as of individuals captured via DNA from hair-snags to estimate population sizes during each year of a 9-year study using a Jolly-Seber approach and estimated individual λs as $N_{t+1}/N$. However, mark–recapture approaches generally provide limited information about why the population did what it did. Given only mark–recapture data, we generally lack information on the age-specific life-history characteristics of the population that produced the observed growth, and thus have limited scope for additional inference.

Our focus here is on the first sort of analysis, in which animals are captured, marked, and followed over time, with the objective of using reproductive and survival rates to estimate λ. Provided age-specific vital rates, bear researchers have used dynamic life tables (e.g., McLoughlin et al. 2003, Harris et al. 2006), Leslie matrices (Bales et al. 2005, Garshelis et al. 2005), or stage-structured population matrices (e.g., Hostetler et al. 2009) to generate the asymptotic rate of growth. Although differing in detail, these approaches are close-cousins, and all, in the words of Doak et al. (2005:1154), are "data hungry."

Because reproductive rates are low, most bear populations are biologically limited to slower increases than the ungulate populations that are typically the object of game managers' interest. Although biologically possible, rapid declines in bear populations are also rare, in part because adults are intelligent animals who often find ways to survive even in the face of deteriorating environments, and in part because hunting mortality is monitored and regulated in managed populations. Given the amount of work normally required to produce a demographic estimate of λ, we are not surprised that biologists often react to this uncertainty with frustration — and managers react with something akin to Kübler-Ross' 5 stages of grief! We would like to know more about study designs and sampling strategies that optimize resources spent, maximizing the chance that a demographic study will produce an estimate of λ with acceptable precision (i.e., minimizing the chance that even the distinction between population increase and decline cannot be made confidently).

We know from theory as well as empirical studies that vital rates are not equal in their contribution to the asymptotic population growth rate. Although the specifics have varied, the overall pattern among bear populations, as in all long-lived species, is that elasticity of adult survival rates are highest and that of reproductive rates lowest (Eberhardt et al. 1994, Hovey and McLellan 1996, Heppell et al. 2000, Freedman et al. 2003, Garshelis et al. 2005, Harris et al. 2006). We also know, both from life-history theory and empirical work, that the magnitude of temporal variation in these vital rates displays the reverse trend: adult survival tends to be relatively invariant with environmental conditions (although is clearly responsive to human-caused mortality), and reproductive rates are more plastic, varying with yearly conditions, population density, and probably other factors we don't think to measure (Gaillard et al. 2000). This tension between focusing on life-history traits with the most influence on population trajectory and on traits that actually vary more has been well explored in the literature (e.g., Mills et al. 1999, de Kroon et al. 2000, Wisdom et al. 2000).

However, even with an understanding of these dynamics, it is not intuitive how to best allocate resources in a study to optimize the precision of λ, even if the bottom-line financial and logistical constraints are set. Does one do better to focus effort on sampling for survival rates of adult females (who we know act as the engine of population growth rate, but who often survive at similar rates regardless of circumstances)? Or does one do better to allocate more effort on estimating survival of young, or on reproductive rates (which generally tend to vary more, but have less influence on population growth)? Allocation strategies may also vary depending on how the investigator models age classes of the population of interest (e.g., whether or not a separate sub-adult age class is recognized), or on the expected magnitude of variation in vital rates of these age classes.

For studies of free-ranging bears, the issue is not merely a matter of which animals one attempts to capture: field protocols also vary, depending on the focus. Once radiotagged, determining whether a female has died during a monitoring interval is relatively straight forward. Most radio beacons include a mortality indicator, and even if not, movement of the animal can often serve to indicate whether the animal has died. In contrast, cub and yearling grizzly bears (*Ursus arctos*) are rarely captured and marked by researchers. Instead, their survival rate is usually inferred from repeated visual observations of the family, and is thus indirect. It usually requires more intensive observation to determine the presence and size of a litter than to determine whether the female is still alive. Consequently, reproductive data are often collected less frequently than survival data, particularly in forested environments. For American black bears (*U. americanus*), many investigators monitor juveniles directly (e.g., Hostetler et al. 2009) and others (e.g., Hebblewhite et al. 2003, Clark and Eastridge 2006) use repeated observations of family groups as in grizzly bear studies. For both species, data on reproduction and juvenile survival accumulate more slowly than do data on adult survival because bears reproduce only at intervals of 2, 3, or even more years, and young are rarely monitored without also monitoring their mothers.

Our objective was to explore the inter-relationships between sample size of animals followed, duration of study, and allocation of monitoring effort among adult females and their litters, and how each affect the precision of estimates of λ. We did so via simulating the dynamics of typical grizzly and black bear populations in simple matrix formulations, varying sample sizes and allocation of effort.

## Methods

We used the approximate formula developed by Doak et al. (2005) to relate sample sizes (in terms of individual animals sampled/year and duration of monitoring) to the precision in estimated rate of growth, λ (Appendix A). This formula uses all the information available from a population projection matrix (vital rate means, sampling variances, process variances, and correlations among all) to solve for the variance of ln (λ), incorporating the sensitivity of each vital rate for that particular matrix. The approximate formula has been shown to be accurate unless temporal (process) variances of individual vital rates are very high (Doak et al. 2005: Appendix C). One disadvantage is that it cannot deal with possible serial correlation of vital rates (e.g., non-independence among successive years). Serial correlation in fecundity could arise if some environmental event causes reproduction to become synchronized (i.e., most females having litters in some years and caring for dependent young in others) and if variance of inter-litter interval is small. However, empirical evidence of serial correlation in bear vital rates is rare (but see McLaughlin et al. 1994). Because any projection of future precision must use educated guesses of all the vital rates that will apply in the future (as well as make hypotheses regarding future sample sizes), we viewed this, as well as other minor theoretical problems that Doak et al. (2005) admit characterize their formulation, as inconsequential for our purposes.

We selected 4 published studies of bear populations and created Leslie matrices for each using published vital rates in program Lamvaresti.m (using MATLAB 7.9.0.529, Natick, Massachusetts, USA; see Doak et al. 2005; Supplement, Ecological Archives E086-062-S1), which solves Eq. A1 (Appendix A). For each combination of vital rates and samples sizes, we calculated SE (ln λ) as $\sqrt{Var(\ln \lambda)}$, and, assuming normality, 90% confidence intervals as $\ln \lambda \pm 1.64 \times SE(\ln \lambda)$. To express these values in terms of λ, we exponentiated each confidence limit. For each population's matrix (Table 1), we conducted experiments varying sample sizes for each vital rate and the duration of monitoring.

### Bear population case studies

As examples on which to apply our hypothetical sample sizes and sampling designs, we chose 4 bear populations (2 grizzly bear, 2 black bear) which had been subject to monitoring using radiotracking and demographic analyses in published or ongoing studies. These 4 provided a variety of age–class categorization and varied in the magnitude of variance reported for vital rates (either estimated process variances or total variance, see below). These 4 case studies (Table 1) were:

1. The Greater Yellowstone Ecosystem (Yellowstone) grizzly bear population during 1983–2001, as studied by Schwartz et al. (2006a). In a demographic analysis, Harris et al. (2006) modeled 4 vital rates: cub survival ($s_0$; Schwartz

**Table 1. Vital rates for estimating sample sizes needed for levels of precision in future estimates of λ for 4 bear populations: Greater Yellowstone Ecosystem grizzly bears (Yellowstone; Schwartz et al. 2006a), Northern Continental Divide grizzly bears (Montana; Mace et al., unpublished data), White River National Wildlife Refuge black bears (Arkansas; Clark and Eastridge 2006), and Bow Valley black bears (Alberta; Hebblewhite et al. 2003). In cases where values for fecundity ($m_x$) are provided (because these were values calculated from field data), the appropriate $f_x$ values were used in the matrix formulation (Doak et al. 2005). Symbols for survival rates follow the convention $s_x$, where $x$ = age.**

| Vital rate | Mean | SE | Variance |
|---|---|---|---|
| Yellowstone grizzly bears | | | |
| $m_x$ | 0.318 | 0.0245 | 0.00060 |
| $s_0$ | 0.640 | 0.0322 | 0.00104 |
| $s_1$ | 0.817 | 0.0431 | 0.00186 |
| $s_{2+}$ | 0.950 | 0.0134 | 0.00018[a] |
| Montana grizzly bears | | | |
| $m_x$ | 0.367 | 0.0453 | 0.00205 |
| $s_0$ | 0.612 | 0.1076 | 0.01159 |
| $s_1$ | 0.682 | 0.1322 | 0.01748 |
| $s_{2-4}$ | 0.852 | 0.0789 | 0.00622 |
| $s_{5+}$ | 0.953 | 0.0207 | 0.00043 |
| Arkansas black bears | | | |
| $m_x$ | 0.685 | 0.1358 | 0.01845[a] |
| $s_0$ | 0.431 | 0.2040 | 0.04162[a] |
| $s_{1-3}$ | 0.923 | 0.0410 | 0.00168[a] |
| $s_{4+}$ | 0.923 | 0.0200 | 0.00040[a] |
| Alberta black bears | | | |
| $f_x$ | 0.390 | 0.0900 | 0.00810 |
| $s_0$ | 0.640 | 0.1070 | 0.01145 |
| $s_1$ | 0.670 | 0.1420 | 0.02016 |
| $s_{2-3}$ | 0.765 | 0.1490 | 0.02220 |
| $s_{4+}$ | 0.835 | 0.1060 | 0.01124 |

[a]Estimated process variance

et al. 2006c), yearling survival ($s_1$; Schwartz et al. 2006c); fecundity ($m_x$; Schwartz et al. 2006b) and adult survival ($s_{2+}$; Haroldson et al. 2006). For adult survival, we used the data set $S_C$ of Haroldson et al. (2006), in which animals with unresolved fates were censored following last radio contact.

2. The Northern Continental Divide (Montana) grizzly bear population in northern Montana, studied by Mace et al. (unpublished data) during 2004–09. These authors, in addition to the vital rates above, considered a separate subadult age class (ages 2–4), with adulthood considered to begin at age 5.
3. The White River National Wildlife Refuge (Arkansas) black bear population, 1998–2003, in Arkansas studied by Clark and Eastridge (2006). In their use of the stochastic simulation program RISKMAN (Taylor et al. 2001), these authors considered 4 vital rates, but rather than a yearling survival rate ($s_1$), considered a subadult ($s_{1-3}$) class, with adulthood considered to begin at age 4.
4. The Bow Valley (Alberta) black bear population in Banff National Park, Alberta, Canada, 1994–2000, studied by Hebblewhite et al. (2003). These authors structured their demographic modeling similarly to that of Mace et al. (unpublished data), except that the subadult class was considered ages 2–3, with adults defined as 4 and older.

Estimation of variance to be expected in future demographic monitoring requires guesses (i.e., rough estimates from other studies or similar species) at the mean, temporal (process) variances, and correlations among each of the vital rates. It seemed intuitive for us to use the existing means for each of the vital rates. Although we should generally expect to observe temporal correlations among some pairs of vital rates (e.g., cub and juvenile survival, or juvenile survival and fecundity may co-vary by year), it is rarely documented in field studies. This may be because variance components are not often identified (and thus correlations among processes may be masked by sampling variance). Because we had no available information on temporal correlations, we modeled all vital rates as uncorrelated for the bulk of our work and investigated likely effects of temporal correlation in a separate set of simulations (Appendix B).

That left the problem of estimating temporal (process) variation for survival and fecundity rates. In 2 of our case studies (Yellowstone and Arkansas), investigators were able to remove sampling variation from some or all vital rates and thus develop estimates of process (i.e., temporal) variance, the appropriate value to use in evaluating sample sizes (Doak et al. 2005). In the other 2 studies (Montana and Alberta), small sample sizes precluded investigators from conducting variance components analyses; thus, they reported only estimates of total variance in vital rates. We recognize the utility of separating sampling from process variance, but we also acknowledge that it cannot always be accom-

**Table 2. Annual sample sizes used to project rates of growth from demographic rates for bear populations in North America from published studies. Numbers in parentheses are sample sizes proportional to number of adult females. In some cases, sample sizes were approximated from indirect information provided in the sources and should be viewed as rough because details of data censoring did not allow precise calculations.**

| Location | Duration of study (years) | Adult females/yr | Litter sizes/yr | Cubs/yr | Yearlings/yr | Source |
|---|---|---|---|---|---|---|
| Grizzly bear | | | | | | |
| Yellowstone | 19–20[a] | 23.0 | 5.1 (0.22) | 6.8 (0.30) | 5.2 (0.23) | Schwartz et al (2006a) |
| Alberta | 9 | 12.9 | 4.2 (0.33) | 5.9 (0.46) | 3.6 (0.28) | Garshelis et al. (2005) |
| Northwest Territories | 12 | 12.2 | 2.9 (0.24) | 4.7 (0.40) | 4.2 (0.35) | McLoughlin et al. (2003) |
| Montana | 6 | 20.4 | 5.0 (0.25) | 10.0 (0.49) | 5.7 (0.28) | Mace et al. (unpublished) |
| Alaska | 11 | 22.8 | 7.4 (0.32) | 11.7 (0.51) | [b] | Kovach et al. (2006) |
| British Columbia | 15 | 7.9 | [b] | 2.9 (0.37) | 2.3 (0.30) | Hovey and McLellan (1996) |
| Black bear | | | | | | |
| Ontario | 11 | 35.9 | 11.9 (0.33) | 22.8 (0.64) | 6.3 (0.18) | Obbard and Howe (2008) |
| Florida | 4–7[a] | 22.8 | | 12.5 (0.55) | [c] | Hostetler et al. (2009) |
| ONF study area | | [b] | [b] | 6.5 | [c] | Hostetler et al. (2009) |
| Lynn study area | | [b] | [b] | 6.0 | [c] | Hostetler et al. (2009) |
| Alberta | 6 | 8.6[d] | 2.5 (0.29) | 3.7 (0.43) | 2.0 (0.23) | Hebblewhite et al. (2003) |
| Arkansas | 5–7[a] | 31.1 | 15.4(0.50) | 3.5 (0.11) | [c] | Clark and Eastridge (2006) |

***Study details***

Yellowstone. Years of monitoring: adult survival (19); reproduction and juvenile survival (20). Sample sizes: adult females (mean = 23/yr), litter sizes (34), litters (102), dependent young (137), cubs (137); yearlings (105).

Alberta grizzly bears. Years of monitoring: 9. Sample sizes: adult females (115.8 bear-years), litters (38), cub survival (53), yearling survival (32).

Northwest Territories. Years of monitoring: 12. Sample sizes: adult females (146 bear-years), litters (35), cubs (57), yearlings (51).

Montana. Years of monitoring: 6. Sample sizes: adult females (1,472 bear months), litters (30), cub survival (60), yearling survival (34).

Alaska. Years of monitoring: 11. Sample sizes: adult females (251 bear-years), litters ( 81), cubs (129).

British Columbia. Years of monitoring: 15. Sample sizes: adult females (118.1 bear years), cub survival (44), yearling survival (35).

Ontario. Years of monitoring: 11; litters, 9; Sample sizes: adult females (395 bear-seasons), litters (107), cub survival (251), yearling survival (69).

Florida. Years of monitoring: adult survival, 7; litter size, 6; cub survival, 4. Sample sizes: adult females (58,382 days ~ 160 bear-years).

Alberta black bears. Years of monitoring: 6. Sample sizes: adult bears ( 51.8 bear-years), litters (15), cub survival (22), yearling survival (12).

Arkansas. Years of monitoring: adult survival, 5; reproduction, 7. Sample sizes: adult females (1,863.6 bear-months ~ 155 bear-years), cub survival (6), litters (108), cub survival (21).

[a]Depended on data collected.
[b]Unclear from source.
[c]Not estimated in this study.
[d]Includes males.

plished (e.g., Howe et al. 2007). Rather than view studies lacking estimates of process variance as useless for our purposes, we viewed them as representatives of situations in which vital rate variances would be large. Thus, we used the total variance for vital rates in these 2 case studies.

### *Sample sizes and sampling strategies*

To evaluate the joint effects of sampling intensity and length of monitoring period on the precision of estimated $\lambda$, we conducted experiments for each case study in which sample sizes of 10, 20, and 30 radiocollared female bears were monitored annually over 2–20 years. We also varied the number of litters documented, cubs monitored, and yearlings monitored to reflect proportions typically encountered in bear studies (Table 2).

To illustrate trade-offs in the effort expended in capturing and monitoring adult females and following animals already marked for reproduction and juvenile survival data, we conducted experiments in which we compared the relative increase in precision obtained by increasing litter monitoring (given a fixed number of females) with that obtained by increasing the number of females monitored (for a fixed number of litters monitored).

## Results

We express precision in terms of the width of the confidence interval surrounding the estimated as-

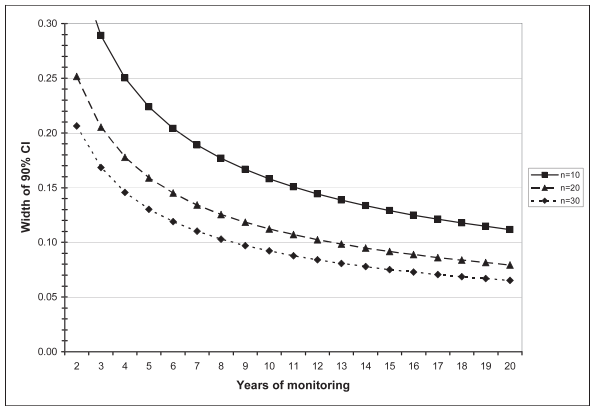


**Fig. 1. Precision (expressed as width of 90% confidence intervals) as a function of years of monitoring for a grizzly bear population with means and variances of vital rates similar to that documented for the Greater Yellowstone Ecosystem population, 1983–2001 (Schwartz et al. 2006a). Sample sizes are annual numbers of adult females monitored (squares = 10, triangles = 20, diamonds = 30); in each case, annual samples sizes contributing to estimates of reproductive rate are 20%, cub survival 30%, and yearling survival 20% of the adult females monitored. These sample size proportions are similar to those reported by Schwartz et al. (2006a); see also Table 2.**

ymptotic growth rate ($\lambda$) for specified study durations and for mean annual sample sizes for each vital rate monitored.

### *Sample sizes and years of monitoring*

Confidence interval widths narrowed as the number of years included in calculations increased (Fig. 1). Given sample sizes and vital rate variances similar to our case studies, it is impossible to achieve high precision with just a few years of monitoring. The greatest improvement in precision comes early, with increasing monitoring from 3 to ~7 years, and additional, substantial improvements coming from increasing the monitoring to ~10 years. Precision continues to increase with increasing duration after 10 years, but at a slower rate. Also evident is that greater increases in precision come from increasing sample sizes that are somewhat low (e.g., 10–20 females/year) than from increasing sample sizes if they are already somewhat larger.

As an example, if a management question is whether the Yellowstone population has truly grown (90% certainty that true $\lambda > 1.0$, i.e., the confidence interval, centered on $\lambda$ does not overlap 1.0) given a point estimate of approximately 6.4% annual growth (Harris et al. 2007), these projections suggest that the question could be answered in as few as 6 years if 30 radiomarked females/year are monitored for survival with 6/year also monitored for reproduction, 9/year for cub survival, and 6/ year for yearling survival. With these sample sizes reduced to 20 marked animals/year (and other samples reduced proportionally), the same assurance would require approximately 9 years.

There are diminishing returns with increased sampling; that is, there are practical limits to the precision that can be achieved under any realistic scenario. Under most realistic scenarios, 90% confidence intervals of width <0.05 (e.g., if estimated $\lambda$ = 1.0, CI of ~ 0.975–1.025) are difficult to achieve in bear studies of <20 years (Fig. 1).

Directly comparing precision achieved among published studies is confounded by differences not only in study duration and mean annual sample sizes, but also by the magnitude of variances in vital rates and whether process-only or total variance is estimated. To illustrate the effect of vital rate variances on the precision achievable for $\lambda$, we artificially fixed study duration and sample sizes as equal for all 4 case studies (Table 3). Confidence intervals were narrowest for the Yellowstone grizzly bear population data and widest for the Alberta

**Table 3. Widths of 90% confidence intervals surrounding asymptotic rates of growth ($\lambda$) of 4 bear populations based on means and variances of vital rates as published. Annual sample sizes of animals monitored for adult female survival, subadult female survival, litter size, cub survival, and yearling survival were artificially constrained to allow for direct comparisons among studies. In all cases, the duration of monitoring was simulated as 10 years. The Yellowstone grizzly bear study did not recognize a sub-adult age class; the Arkansas black bear study considered yearlings as subadults.**

| | Adults | Subadults | Litters | Cubs | Yearlings | 90% CI width |
|---|---|---|---|---|---|---|
| **Yellowstone grizzly bears** | 30 | — | 10 | 10 | 10 | 0.07641 |
| **Montana grizzly bears** | 20 | 10 | 10 | 10 | 10 | 0.08123 |
| **Arkansas black bears** | 30 | 10 | 10 | 10 | — | 0.08533 |
| **Alberta black bears** | 20 | 10 | 10 | 10 | 10 | 0.12030 |

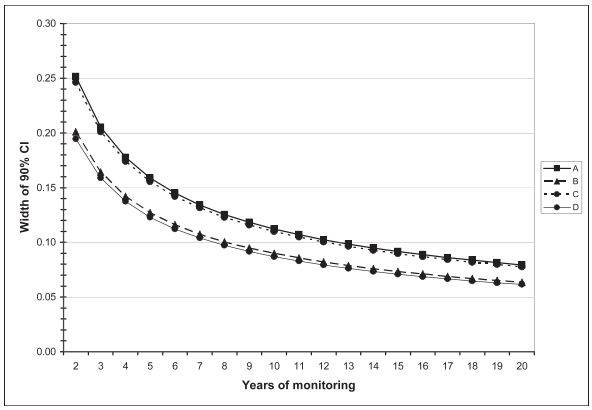


**Fig. 2. Precision (expressed as width of 90% confidence intervals) as a function of years of monitoring for a grizzly bear population with means and variances of vital rates similar to that documented for the Greater Yellowstone Ecosystem population, 1983–2001 (Schwartz et al. 2006a). All isoclines were generated from simulations with 20 adult females and 4 yearlings monitored annually for survival. Other sample sizes are as follows. A: $m_x = 4$, $s_0 = 6$; B: $m_x = 8$, $s_0 = 6$; C: $m_x = 4$, $s_0 = 12$; D: $m_x = 8$, $s_0 = 12$.**

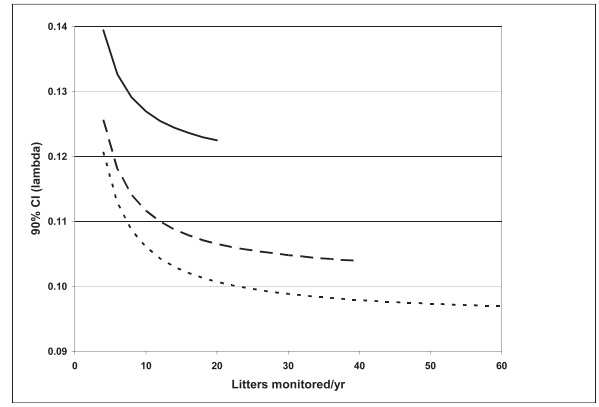


**Fig. 3. Precision (expressed as width of the 90% CI) of λ as a function of increasing the sample size of litters monitored/year for 20, (solid), 40 (long dash), or 60 (short-dash) animals monitored/year (including all rates) over a 10-year monitoring duration. Monitoring litters is assumed to provide data on the reproductive parameter in a Leslie matrix ($f_x$), cub survival ($s_0$), and yearling survival ($s_1$). Projections are based on demographic rates for Alberta black bears (Hebblewhite et al. 2003).**

black bear population data. These results follow generally from the relatively precise estimates of independent bear survival (process variation only) and reproduction in Yellowstone compared with those achieved in the Alberta study.

Adding temporal correlations among pairs of vital rates produced almost imperceptible increases in the variance in λ. Even under an extreme scenario in which all rates were highly correlated with each other, standard errors of λ increased by trivial amounts (Appendix B).

### *Monitoring female survival versus monitoring litter sizes and juvenile survival*

For a set number of adult females monitored, adding to the sample of those monitored for reproduction and litters monitored for survival increased precision (Fig. 2). However, as seen in the Yellowstone grizzly bear example, doubling the number of cubs monitored for survival increased precision only slightly (compare line A with C, and line B with D). A much greater proportional increase in precision was achieved by doubling the sample size used to estimate $m_x$ (compare line A with B, and line C with D). Extended parental care in bears limits the number of litters available under any conceivable sampling protocol.

Comparing a sampling procedure that routinely yields data leading toward estimates of $m_x$, cub survival, and sub-adult survival from intensive monitoring of females with one in which reproductive data are rarely obtained, one sees that relatively rapid increases in precision can be achieved from the former when starting from low sample sizes. In the Alberta black bear case study (Hebblewhite et al. 2003), the per capita improvement in precision from increasing the sample size of litters monitored is greater than that of increasing the number of marked females whose litters are not then followed (Fig. 3). Using the Yellowstone data as an example, if 20 animals are captured, collared, and followed over 10 years, but only 6 can be monitored closely enough for litter size and juvenile survival to be known annually, the 90% confidence interval width around λ is expected to be approximately 0.1488 (Fig. 4, point A). If 6 additional animals could be captured (but only the original 6 of the 26 monitored to determine litter size and juvenile survival), expected confidence interval width would decline to approximately 0.1476 (Fig. 4, point B). However, if instead of capturing 6 more animals, 6 more of the original 20 could be monitored intensively (increasing to 12 the number of marked females closely monitored,

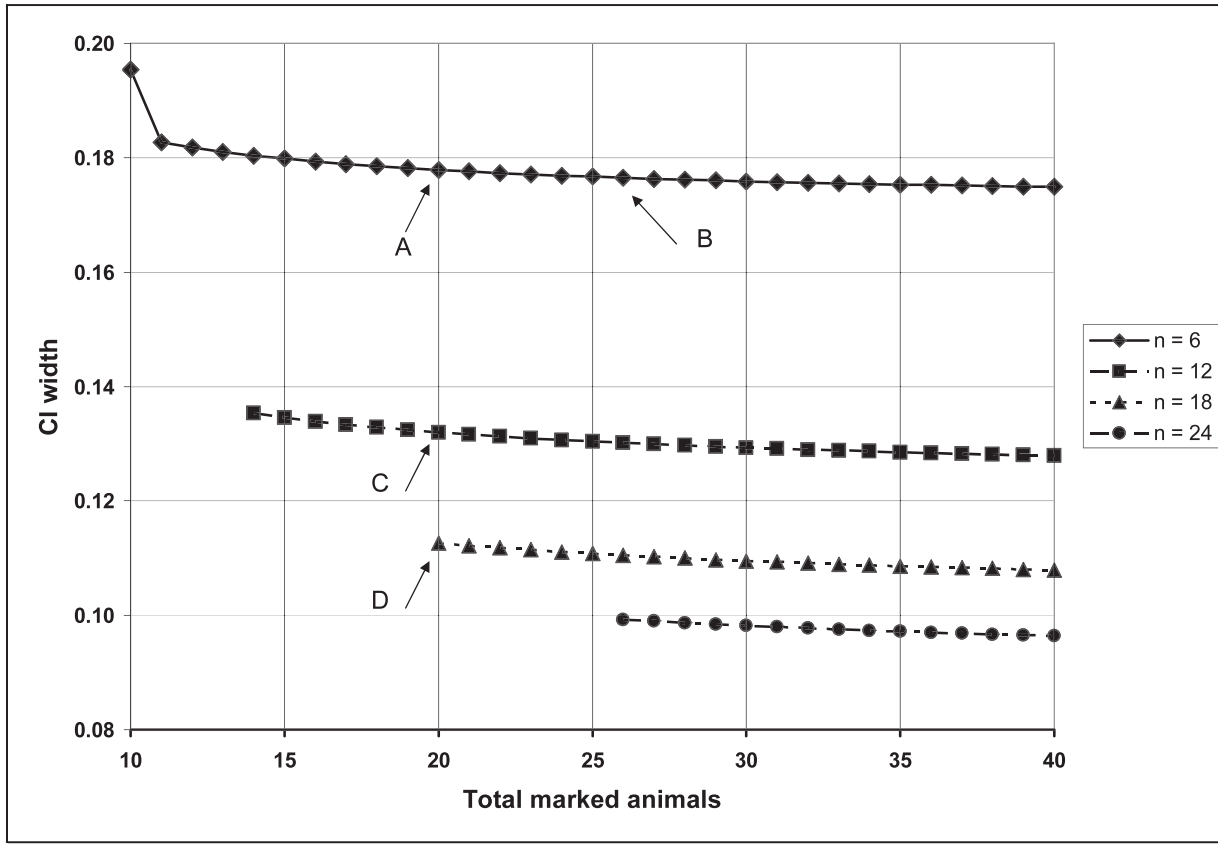


**Fig. 4. Precision (expressed as width of the 90% CI) of λ as a function of increasing the sample size of radiomarked adult females (from 10 to 40) monitored annually for survival over a 10-year period, where various numbers of these animals ($n$ = 6 [diamonds], 12 [squares], 18 [triangles], or 24 [circles]) are also monitored closely enough that reproduction ($m_x$) and juvenile survival ($s_0$, $s_1$) can be documented annually. The assumption is that in any given year, 1/3 of these females will produce cubs (and thus contribute to estimates of $m_x$), 1/3 will have cubs (and thus contribute to estimates of $s_0$), and 1/3 yearlings (and thus contribute to estimates of $s_1$). This scenario uses vital rates from the Yellowstone population (1983–2002), with high process variance. This scenario did not allow for the possibility that a female would be monitored solely for reproduction or juvenile survival, while not also obtaining information on her own survival. See text for explanation of points A, B, C, and D.**

black squares), the expected 90% confidence interval width around λ would drop to approximately 0.1104 (Fig. 4, point C), increasing precision by about a third. If 18 of 20 marked animals could be monitored for litters and juvenile survival (triangles), precision would increase further (confidence interval width would drop to about 0.0942; Fig. 4, point D).

## Discussion

Based on these 4 case studies, our results suggest that managers should expect confidence limits around λ generated from demographic analyses of bear populations to be broad unless sample sizes are larger than are typically available, or unless >10 years of data are evaluated. When point estimates of $|1-\lambda|$ are <0.5 the width of our projected confidence intervals (e.g., Fig. 1–4, Tables 3, 4), the direction of population change (i.e., growth or decline) will remain uncertain.

Fortunately, precision of λ appears relatively insensitive to differences in the magnitude of variance in vital rates, at least among the 4 case studies we examined. Our work suggests that removing sampling variance will improve the precision of λ, and is thus always worth the attempt. However, even if successful, the residual process variance will likely be high enough to prevent highly

**Table 4. Widths of 90% confidence intervals surrounding asymptotic rates of growth (λ) of 2 bear populations based on means and variances of vital rates as published. Annual sample sizes of animals monitored were varied artificially to contrast sampling strategies. In all cases, the duration of monitoring was simulated as 10 years. The Arkansas black bear study considered yearlings as subadults.**

| | Adults | Subadults | Litters | Cubs | Yearlings | 90% CI width |
|---|---|---|---|---|---|---|
| **Montana grizzly bears** | 20 | 10 | 5 | 10 | 5 | 0.09896 |
| | 20 | 10 | 5 | 15 | 5 | 0.09808 |
| | 20 | 10 | 5 | 20 | 5 | 0.09765 |
| | 20 | 10 | 10 | 10 | 5 | 0.08353 |
| | 20 | 10 | 10 | 15 | 5 | 0.08249 |
| | 20 | 10 | 10 | 20 | 5 | 0.08197 |
| | 20 | 10 | 10 | 10 | 10 | 0.08123 |
| | 20 | 10 | 10 | 15 | 10 | 0.08016 |
| | 20 | 10 | 10 | 20 | 10 | 0.07963 |
| **Arkansas black bears** | 30 | 10 | 10 | 10 | — | 0.08533 |
| | 30 | 10 | 10 | 20 | — | 0.08157 |
| | 30 | 10 | 10 | 30 | — | 0.08028 |
| | 30 | 10 | 20 | 10 | — | 0.08117 |
| | 30 | 10 | 30 | 10 | — | 0.07973 |
| | 30 | 20 | 30 | 10 | — | 0.07746 |

precise estimates of λ. Relatively large samples of marked animals and long monitoring periods will generally be needed to achieve high precision estimates of λ. (Of course, these larger sample sizes are exactly what will facilitate being able to use methods to account for sampling variance).

Less intuitive are our results that increasing the sample size of litters monitored will often be a more efficient way of increasing the precision of λ than increasing the number of marked females. This may be surprising because the elasticity of adult female survival for long-lived species such as bears is always much higher than it is for reproductive and juvenile survival parameters (Eberhardt et al. 1994, Freedman et al. 2003, Garshelis et al. 2005, Harris et al. 2006, Hostetler et al. 2009). However, as has been shown for other taxa (e.g., Wisdom and Mills 1997) and recently corroborated for black bears (Mitchell et al. 2009), variation in juvenile survival and recruitment may exert a greater influence on λ than variation in adult female survival because the latter tends to have low variance. Thus, investments in estimating recruitment and juvenile survival may yield high returns, particularly in cases where the sample of adult females is adequate but fewer litters are generally monitored. A more detailed analysis of this trade-off would require evaluating the costs of capture/marking per female against the costs of monitoring females already marked, which will vary with study logistics. In most circumstances, we would imagine that such an economic analysis would not alter the fundamental relationships between precision and sample size (Fig. 3, 4).

Sample sizes we used in this analysis should be seen as approximate, useful as heuristic rather than strict guidelines. The approximation of Doak et al. (2005) required that we specify fixed numbers of animals monitored for each rate during entire yearly periods in simulations, but quantifying the sampling efforts from field studies of bears as they actually contribute to the precision of vital rates is difficult. Sample sizes generally vary across years; we've approximated this by expressing results in terms of mean annual sample sizes across the study period. Further, in most cases, animals enter and leave the sample within any given year (due to staggered entry, mortality, radio-failure, or other reasons for censoring observations).

We simplified the issue of estimating reproductive rates for bears, with their multi-year reproductive cycles, by focusing on sample sizes of litters. Information leading to $m_x$ (or $f_x$) is also collected when monitoring females in years other than those when she produces a litter, but in general, it takes $>1$ year to obtain a single data point. Theoretically, the number of cubs monitored for survival can approach the number of adult females monitored (e.g., a typical scenario for black bears in which 2 cubs are produced every second year), but field logistics evidently conspire to make this rare (e.g., Table 2, suggests that at best, 0.64 cubs were monitored per adult female). Cub survival has also

been found to be non-independent of litter (i.e., cubs more likely to share the fate of their litter-mate than of a randomly selected cub) in most studies where it has been examined. Failure to account for this would result in artificially reducing the variance of $s_0$. However, most investigators have adopted approximate solutions to this by using a variance inflation factor (e.g., $\hat{c}$) to correct for over-dispersion; consequently, we felt justified in expressing sample sizes for $s_0$ in terms of cubs rather than litters.

We prefer to present figures displaying 90%, rather than 95%, confidence intervals. The latter are the standard, and familiarity with '95%' may provide comfort. Note however, that for bears, focus is usually only on the lower tail of the distribution of λ, i.e., obtaining some level of certainty that the population is not declining. With 95% confidence intervals, this means that (assuming accuracy of the parameters and reasonableness of the model) there would be only a 2.5% chance that the true growth rate did not exceed this level. Acknowledging that prudence would suggest minimizing the chance of erroneously concluding that $\lambda \neq 1.0$ (and thus opting to use 95% confidence intervals), it may be that managers (or the general public) may be comfortable instead with accepting risks of, say, 5% that the population may actually have grown more slowly or quickly than a specific rate (i.e., using a 90% confidence interval).

## Management implications

Managers and policy makers should be aware that monitoring bear populations is inherently imprecise. In most circumstances, demographic modeling of marked bears will require 5 to 10 years before estimates of λ will have confidence limits that even approach 0.10. Larger sample sizes will reduce the monitoring duration required to achieve acceptable precision or reduce the uncertainty around λ given a set time period. Though it is intuitive that adult females drive population growth, the relatively higher variability of recruitment and juvenile survival provides a quantitative rationale for increasing their sampling intensity.

We recommend choosing an approach to estimate λ based on cost-effectiveness, study objectives, the precision in λ required for population management, availability of a long-term research infrastructure, and value-added information beyond study objectives. For Arkansas black bears, Clark and Eastridge (2006) concluded that Pradel modeling was a more cost-effective approach to estimate λ than demographic analyses using projection models because the former required no radiotracking. Stetz et al. (2010) simulated sample designs and sample sizes needed to obtain specified precision of λ using Pradel models based on DNA data from an extensive collection of hair follicles obtained from trees rubbed by grizzly bears and concluded that this approach was also promising. Whether mark–recapture methods (using either live captures or remotely collected DNA) would be more cost-effective than demographic analysis in other situations is beyond the scope of our investigation. With either approach, managers should explicitly state the limitations of extending the resulting estimates of λ beyond the time period and geographic area considered.

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## Literature cited

Bales, S.L., E.C. Hellgren, D.M. Leslie, Jr., and J. Hemphill, Jr. 2005. Dynamics of a recolonizing population of black bears in the Ouachita Mountains of Oklahoma. Wildlife Society Bulletin 33:1342–1351.

Brodie, J.F., and M.L. Gibeau. 2007. Brown bear population trends from demographic and monitoring based estimators. Ursus 18:137–144.

Brongo, L.L., M.S. Mitchell, and J.B. Grand. 2005. Long-term analysis of survival, fertility, and population growth rate of black bears in North Carolina. Journal of Mammalogy 86:1029–1035.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Chichester, UK.

Cherry, S., G.C. White, K.A. Keating, M.A. Haroldson, and C.C. Schwartz. 2007. Evaluating estimators of the numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. Journal of Agricultural, Biological, and Environmental Statistics 12:195–215, 221.

Clark, J.D., and R. Eastridge. 2006. Growth and sustainability of black bears at White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 70:1094–1101.

———, ———, and M.J. Hooker. 2010. Effects of exploitation on black bear populations at White River National Wildlife Refuge. Journal of Wildlife Management 74:1448–1456.

de Kroon, H., J. van Groenendael, and J. Ehrlen. 2000. Elasticities: A review of methods and model limitations. Ecology 81:607–618.

Doak, D.F., K. Gross, and W.F. Morris. 2005. Understanding and predicting the effects of sparse data on demographic analyses. Ecology 86:1154–1163.

Eberhardt, L.L., B.M. Blanchard, and R.R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360–363.

Freedman, A.H., K.M. Portier, and M.E. Sunquist. 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. Ecological Modeling 167:47–64.

Gaillard, J.M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Garshelis, D.L., M.L. Gibeau, and S. Herrero. 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. Journal of Wildlife Management 69:277–297.

Haroldson, M.A., C.C. Schwartz, and G.C. White. 2006. Survival of independent grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–42 in C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. Wildlife Monographs 161.

Harris, R.B., C.C. Schwartz, M.A. Haroldson, and G.C. White. 2006. Trajectory of the greater Yellowstone ecosystem grizzly bear population under alternative survival rates. Pages 45–56 in C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. Wildlife Monographs 161.

———, G.C. White, C.C. Schwartz, and M.A. Haroldson. 2007. Population growth of Yellowstone grizzly bears: Uncertainty and future monitoring. Ursus 18:167–177.

Hebblewhite, M., M. Percy, and R.T. Serrouya. 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. Biological Conservation 112:415–425.

Heppell, S.S., H. Caswell, and L.B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology 81:654–665.

Hostetler, J.A., J.W. McCown, E.P. Garrison, A.M. Neils, M.A. Barrett, M.E. Sunquist, S.L. Simek, and M.K. Oli. 2009. Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. Biological Conservation 112:415–425.

Hovey, F.W., and B.N. McLellan. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74:1409–1416.

Howe, E.J., M.E. Obbard, and J.A. Schaefer. 2007. Extirpation risk of an isolated black bear population under different management scenarios. Journal of Wildlife Management 71:603–612.

Knight, R.R., B.M. Blanchard, and L.L. Eberhardt. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248.

Kovach, S.D., G.H. Collins, M.T. Hinkes, and J.W. Denton. 2006. Reproduction and survival of brown bears in southwest Alaska, USA. Ursus 17:16–29.

McDonald, J.E. , Jr., and T.K. Fuller. 2001. Prediction of litter size in American black bears. Ursus 12:93–102.

McLaughlin, C.R., G.J. Matula, Jr., and R.J. O'connor. 1994. Synchronous reproduction by Maine black bears. International Conference on Bear Research and Management 9(1):471–479.

McLoughlin, P.D., M.K. Taylor, H.D. Cluff, R.J. Gau, R. Mulders, R.L. Case, S. Boutin, and F. Messier. 2003. Demography of barren-ground grizzly bears. Canadian Journal of Zoology 81:294–301.

Mills, L.S., D.F. Doak, and M.J. Wisdom. 1999. Reliability of conservation actions based on sensitivity analysis of matrix models. Conservation Biology 13:1–15.

Mitchell, M.S., L.B. Pacifici, J.B. Grand, and R.A. Powell. 2009. Contributions of vital rates to growth of a protected population of American black bears. Ursus 20:77–84.

Obbard, M.E., and E.J. Howe. 2008. Demography of black bears in hunted and unhunted areas of the boreal forest of Ontario. Journal of Wildlife Management 72:869–880.

Schwartz, C.C., M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. 2006a. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. Wildlife Monographs 161.

———, ———, AND S. CHERRY. 2006b. Reproductive performance of grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. Pages 18–23 in C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. Wildlife Monographs 161.

———, ———, AND G.C. WHITE. 2006c. Survival of cub and yearling grizzly bears in the greater Yellowstone ecosystem, 1983–2001. Pages 25–31 in C.C. Schwartz, M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. Temporal, spatial and environmental influences on the demographics of grizzly bears in the greater Yellowstone ecosystem. Wildlife Monographs 161.

———, ———, S. CHERRY, AND K.A. KEATING. 2008. Evaluation of rules to distinguish unique female grizzly bears with cubs in Yellowstone. Journal of Wildlife Management 72:543–554.

STETZ, J.B., K.C. KENDALL, AND C. SERVHEEN. 2010. Evaluation of bear rub surveys to monitor grizzly bear population trends. Journal of Wildlife Management 74:860–870.

TAYLOR, M.K., M. OBBARD, B. POND, M. KUC, AND D. ABRAHAM. 2001. RISKMAN: Stochastic and deterministic population modeling RISK MANagement decision tool for harvested and unharvested populations. Government of Nunavut, Iqualuit, Nunavut Territory, Canada.

WISDOM, M.J., AND L.S. MILLS. 1997. Sensitivity analysis to guide population recovery: Prairie chickens as an example. Journal of Wildlife Management 61:302–312.

———, ———, AND D.F. DOAK. 2000. Life stage simulation analysis: Estimating vital-rate effects on population growth for conservation. Ecology 81:628–641.

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## Appendix A

The approximation for the variance of the natural logarithm of the stochastic (i.e., uncertain) rate of growth ($\hat{\lambda}_s$) derived by Doak et al. (2005:1160) is

$$\mathrm{Var}\left(\ln \hat{\lambda}_s\right) = \sum_i \mathrm{Var}(\hat{v}_i)\left(\frac{\partial \ln \lambda_s}{\partial_{v_i}}\right)^2 + \frac{1}{\lambda_1^4}\sum \mathrm{Var}(\hat{\sigma}_{i,E})\left(\sum_j S_i S_j \rho_{i,j}\sigma_{j,E}\right)^2 + \frac{1}{\lambda_1^4}\sum \mathrm{Var}\left(\hat{\rho}_{i,j}\right)\left(S_i S_j \sigma_{i,E}\sigma_{j,E}\right)^2 \quad \text{(Eq. A1)}$$

Quoting Doak et al. (2005:1160), $S_i$ is the sensitivity of the growth rate predicted by the mean matrix, $\lambda_1$, to changes in $\hat{v}_i$ (vital rates, e.g., survival of a given age-class), and $\partial \ln \lambda_s/\partial v_i$ is the sensitivity of the log-stochastic growth rate to the mean vital rate $v_i$. $\mathrm{Var}(\hat{v}_i)$, $\mathrm{Var}(\hat{\sigma}_{i,E})$, and $\mathrm{Var}(\hat{\rho}_{i,j})$ are approximations for the sampling variation in estimated means, variances, and correlations of the vital rates, respectively, and are where limited sampling has its influence. More statistical heavy lifting to further clarify the equation is found in Appendix C of Doak et al. (2005).

Critical to this equation are the sensitivities, which require calculation of various derivatives which would be difficult to do by hand. Thus, the MATLAB program (called Lamvaresti.m) requires the user to specify a matrix structure with estimated vital rates, process variances for each, the correlation matrix among all rates, sample intensity (number of individual animals contributing to estimation of the rate each year), and duration of the study.

## Appendix B

Widths of confidence limits surrounding $\lambda_s = 1.064$ show the effects of specified temporal correlation structures, under various combinations of sampling intensity (animals sampled/yr for a given rate), and duration (number of years), using the Yellowstone grizzly bear population case-study projection matrix. The Yellowstone grizzly bear population matrix used in the main simulations posited zero temporal correlation among vital rates. Correlation structure A posits positive correlations of $\rho = 0.8$ among all pairs involving cub survival, yearling survival, and fecundity, but $\rho = 0.2$ between each of these and adult survival. Correlation structure B posits positive correlations of $\rho = 0.95$ among all possible pairs of vital rates.

| Study duration (yrs) | Adult females monitored for survival/yr[a] | Yellowstone grizzly bear population matrix (no temporal correlation) | Temporal correlation structure A | Temporal correlation structure B |
|---|---|---|---|---|
| 3 | 10 | 0.16695 | 0.16699 | 0.16706 |
| 10 | 10 | 0.09136 | 0.09139 | 0.09143 |
| 20 | 20 | 0.04726 | 0.04729 | 0.04729 |
| 15 | 30 | 0.04604 | 0.04604 | 0.04607 |

[a]See text for assumptions about number of females monitored for litter size and juvenile survival.