Impact of Spatial and Temporal Variation in Calf Survival on the Growth of Elk Populations

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ABSTRACT The realized impact of a vital rate on population growth (λ) is determined by both the relative influence of the vital rate on λ (elasticity) and its magnitude of variability. We estimated mean survival and reproductive rates in elk (*Cervus elaphus*) and spatial and temporal variation in these rates from 37 sources located primarily across the Rocky Mountain region and northwestern United States. We removed sampling variance from estimates of process variance both within and across vital-rate data sets using the variance discounting method developed by White (2000). Deterministic elasticities calculated from a population matrix model parameterized with these mean vital rates ranked adult female survival ($e_{Scow} = 0.869$) much higher than calf survival ($e_{Scalf} = 0.131$). However, process variance in calf survival ($\hat{\sigma}^2_{Scalf} = 0.039$) was >11 times greater than process variance in female survival ($\hat{\sigma}^2_{Scow} = 0.003$) across data sets and 10 times greater on average ($\overline{\sigma}^2_{Scalf} = 0.020$; $\overline{\sigma}^2_{Scow} = 0.002$) within studies. We conducted Life-Stage Simulation Analysis to incorporate both vital-rate elasticity patterns and empirical estimates of variability to identify those vital rates most influential in elk population dynamics. The overwhelming magnitude of variation in calf survival explained 75% of the variation in the population growth rates generated from 1,000 matrix replicates, compared to just 16% of the variation in λ explained by variation in female survival. Variation in calf survival greatly impacts elk population growth and calls into question the utility of classical elasticity analysis alone for guiding elk management. These results also suggest that the majority of interannual variability that wildlife managers document in late-winter and spring elk surveys is attributable to variation in calf survival over the previous year and less influenced by variation in the harvest of females during the preceding autumn. To meet elk population size objectives, managers should consider the inherent variation in calf survival, and its apparent sensitivity to management, in addition to female harvest. (JOURNAL OF WILDLIFE MANAGEMENT 71(3):795–803; 2007)

The current paradigm in sensitivity analysis of using analytical elasticities to identify and target the vital rate that exerts the largest influence on the population growth rate, λ, has greatly improved management efficacy of wildlife populations (Crouse et al. 1987, Heppell et al. 1994, Buenau and Gerber 2004). However, a vital rate's overall impact on population growth is a function of both its influence on λ (elasticity) and its magnitude of change (variability; Wisdom and Mills 1997; Gaillard et al. 1998, 2000; Wisdom et al. 2000; Mills et al. 1999, 2001). In large herbivores, adult survival is consistently identified as the vital rate with the highest elasticity; in contrast, λ is relatively insensitive to calf survival (Escos et al. 1994; Walsh et al. 1995; Gaillard et al. 1998, 2000; Eberhardt 2002; Garrott et al. 2003). In elk (*Cervus elaphus*), adult survival was identified 25 years ago as the stage-specific vital rate that has the greatest influence on the population growth rate (Nelson and Peek 1982). Yet, it is the natural variability in vital rates—not their elasticities—that fundamentally determines the spatial and temporal variation in λ.

Some vital rates are relatively constant over time and space, whereas others are inherently highly variable

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(Gaillard and Yoccoz 2003, Owen-Smith and Mason 2005). Gaillard et al. (1998, 2000) reviewed numerous long-term studies on large herbivores and concluded that annual survival of young varies dramatically relative to the survival of prime-age adults across species, dissimilar environments, and differing cause-specific mortality sources. These studies (and additionally Unsworth et al. 1999) suggested that juvenile survival may be the predominant driver in large herbivore population dynamics. There is growing recognition that vital rates of relatively low elasticity can strongly impact λ if they are highly variable (Mills et al. 1999, Wisdom et al. 2000, Coulson et al. 2005). In elk, calf survival exhibits a high degree of temporal and spatial variability compared to relatively constant rates of adult female survival. In western North America, reported annual rates of elk survival ranged from 0.060 to 0.720 in calves (Singer et al. 1997, Smith et al. 1997, Raithel 2005; Table 1 for complete reference list) and from 0.640 to 0.999 in females (Unsworth et al. 1993, Kunkel and Pletscher 1999, Ballard et al. 2000, Raithel 2005; Table 1). The greatest temporal variation in survival within studies ranged from 0.135 to 0.624 in calves (Singer et al. 1997) and from 0.64 to 0.89 in female elk (Kunkel and Pletscher 1999).

We evaluated how observed variability in elk vital-rates impacts population growth rate using Life-Stage Simulation Analysis (LSA). Life-Stage Simulation Analysis incorpo-

Table 1. Summary statistics for elk survival and pregnancy rates by age class used to parameterize the matrix model for elasticity analysis ($\bar{x}$ vital rates) and Life-Stage Simulation Analysis (mean vital rates and process variance) collected from 37 studies conducted primarily across the Rocky Mountains and northwestern United States between 1935 and 2005.

Vital rate	Total data sources	Total point estimates[a]	Total geographic locations	Total animal yr[b]	Grand $\bar{x}$	Min.	Max.	Total variance S^{2c}	Total process variance $\hat{\sigma}^{2d}$	% of total variance attributable to process	References[e]
Calf survival rate	10	43	13	1,353	**0.354**	0.060	0.720	0.04341	**0.03854**	88.8	16, 22, 25, 26, 29, 32, 34, 35, 36, 37
F survival rate	12	46	13	1,838	**0.873**	0.640	0.999	0.00629	**0.00336**	53.4	17, 18, 19, 20, 21, 24, 27, 28, 29, 30, 33, 34
Yearling survival					0.883				0.00420		
Prime-age survival					0.894				0.00336		
Old-age survival					0.868				0.00336		
Senescent survival					0.724				0.00588		
Yearling pregnancy rate	17	29	15	>1,167	**0.198**	0.000	0.500	0.01902	**0.01508**	79.3	1, 2, 3, 4, 5, 6, 9, 10, 11, 12, 13, 14, 15, 17, 23, 29, 31
Yearling fecundity					0.099						
Prime-age pregnancy rate	12	25	14	2,499	**0.928**	0.781	0.988	0.00236	**0.00126**	53.4	2, 7, 8, 11, 12, 13, 14, 23, 29, 31, 32, 34
Prime-age fecundity					0.464						
Old-age pregnancy rate	7	8	6	254	**0.864**	0.750	0.950	0.00578	**0.00250**	43.3	2, 5, 8, 11, 12, 29, 32
Old-age fecundity					0.432						
Senescent pregnancy rate	6	8	4	115	**0.530**	0.370	0.692	0.01643	**0.00647**	39.4	2, 8, 11, 12, 23, 31
Senescent fecundity					0.265						

[a] Individual point estimates are annual vital rates.
[b] Total animal yr represents the cumulative sample size across studies.
[c] S^2 denotes the total variance (both process and sampling variance).
[d] $\hat{\sigma}^2$ denotes solely process variance present in each vital-rate data set.
[e] 1. Murie (1951); 2. Cheatum and Gaab (1952); 3. Kittams (1953); 4. Buechner and Swanson (1955); 5. Hancock (1957); 6. Blouch and Moran (1965); 7–9. Greer (1965, 1966, 1968); 10. Cole (1969); 11. Flook (1970); 12. Knight (1970); 13. Trainer (1971); 14. Moran (1973); 15. Follis and Spillett (1974); 16. Schlegel (1976); 17. Freddy (1987); 18. Leptich and Zager (1991); 19. Bureau (1992); 20. Unsworth et al. (1993); 21. Stussy et al. (1994); 22. Myers et al. (1996); 23. Noyes et al. (1996); 24. Cole et al. (1997); 25. Singer et al. (1997); 26. Smith et al. (1997); 27. Kunkel and Pletscher (1999); 28. Ballard et al. (2000); 29. Hamlin and Ross (2002); 30. Lubow et al. (2002); 31. Noyes et al. (2002); 32. Zager et al. (2002); 33. Garrott et al. (2003); 34. Raithel (2005); 35. D. Vales, Muckleshoot Indian Tribe, unpublished data; 36. S. M. Barber, University of Minnesota, Saint Paul, personal communication; P. J. White, National Park Service, personal communication; and L. D. Mech, United States Geological Survey, personal communication; 37. S. L. Findholt and B. K. Johnson, Oregon Department of Fish and Wildlife, personal communication.

rates both retrospective mean vital rates and their inherent variability into a simulation-based framework, under the assumption that observed variation in the past is indicative of how vital rates will potentially vary in the future (Wisdom and Mills 1997, Wisdom et al. 2000, Mills et al. 2001). Life-Stage Simulation Analysis is advantageous because a vital-rate specific coefficient of determination (r^2) can be calculated by regressing asymptotic λ on each vital rate, as other rates change simultaneously. The r^2 value associated with each vital rate represents the proportion of the variation in the simulated population growth rates (generated for each matrix replicate) attributable to potential variation in that vital rate (Mills and Lindberg 2002).

Our primary objectives were to: 1) estimate mean elk vital rates and potential variation in each rate across broadly different habitat types, elk population densities, sex ratios, age-structures, predator compositions and densities, climatic conditions, and management regimes; 2) calculate the sensitivity of λ to changes in each vital rate using elasticities; 3) determine the amount of variation in λ explained by variation in each vital rate using LSA; and 4) interpret how these results might be applied to elk management to effectively meet specific population objectives.

METHODS

Construction of the Generalized Matrix Model

We modeled elk life-history with 5 age classes: calves (0 yr old), yearlings (1 yr old), prime-age adults (2–9 yr old), old-age adults (10–14 yr old), and senescent adults ($\geq$15 yr old; Fig. 1). We assigned age-class boundaries to capture known differences in age-specific survival and fecundity, within the constraints of available data sets. We included both an old-age adult and a senescent adult class because declines in elk survival (Houston 1982, Kunkel and Pletscher 1999, Garrott et al. 2003) may occur before reproductive senescence (Cheatum and Gaab 1952, Greer 1966, Flook 1970), as in other large herbivores (Gaillard et al. 2000).

We constructed a female-based, pre–birth pulse, age-structured matrix (Caswell 2000) with a one-year projection interval (15 × 15 matrix; Raithel 2005). We gave equal age-specific survival and fecundity values to all elk within each age class. Following Peek et al. (2002), we used a prebirth census because annual estimates of elk abundance and herd composition are commonly indexed during winter or early spring, preceding the birth of new calves. Therefore, nonzero matrix elements in the top row are a product of the fecundity of mature age classes and calf survival. Females
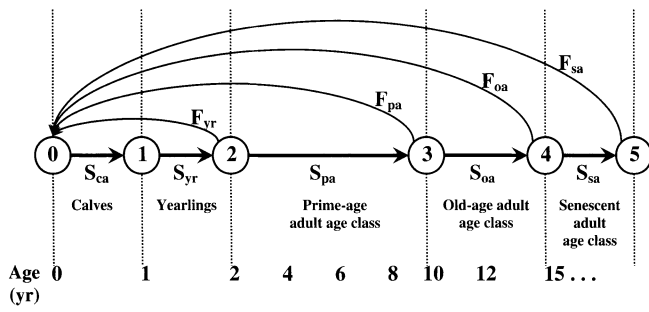
Figure 1. Elk life-history model consisting of 5 age classes: calves (0 yr old), yearlings (1 yr old), prime-age adults (2–9 yr old), old-age adults (10–14 yr old), and senescent adults (≥ 15 yr old). Vital-rate notations are calf survival (S_{ca}), yearling survival (S_{yr}), prime-age adult survival (S_{pa}), old-age adult survival (S_{oa}), senescent adult survival (S_{sa}), yearling fecundity (F_{yr}), prime-age adult fecundity (F_{pa}), old-age adult fecundity (F_{oa}), and senescent adult fecundity (F_{sa}). Graphical representation follows Gaillard et al. (2000).

may become reproductive in their second year (as yearlings); thus, females ≥ 2 years of age are allowed to reproduce in the model. To estimate the production of female young in the fecundity calculations, we assumed a 50:50 sex ratio at birth as is typical for elk when sample sizes are large or data are acquired across multiple years (Johnson 1951, Schlegel 1976). We also assumed that calf survival did not differ between sexes (Singer et al. 1997, Hamlin and Ross 2002, Raithel 2005) and included survival rates from studies that pooled sexes in calf survival estimates.

Fecundity is the product of the pregnancy rate, intrauterine survival rate, and the number of calves born per pregnant female. We set the number of calves born to one in matrix calculations because multiple births occur with a <1% frequency in Rocky Mountain elk (*C. e. nelsoni*; Kittams 1953, Flook 1970). Pregnancy status is commonly assessed during late autumn or early winter by examining harvested females (Cheatum and Gaab 1952; Greer 1966; Noyes et al. 1996, 2002) and during late winter or spring by the presence of pregnancy-specific protein-B (PSPB) in the blood (Zager et al. 2002). Few empirical data existed that quantified intrauterine mortality in brucellosis-free (*Brucella abortus*) elk herds, but it is thought to be uncommon except when maternal females are subject to severe nutritional restrictions during winter or spring (Thorne et al. 1976). Because of the scarcity of empirical estimates of intrauterine survival, we set this rate equal to one following Nelson and Peek (1982); thus, we estimated fecundity in our female-based model as the pregnancy rate multiplied by 0.5 to account for male calves.

Data Sources and Vital-Rate Estimation

We characterized the natural range of variability in elk vital rates attributable to different habitats, population densities, predator compositions and densities, climates, and management regimes from primarily across the Rocky Mountains and northwestern United States. However, we also included studies from Northern Arizona (Ballard et al. 2000) and Michigan, USA (Blouch and Moran 1965, Moran 1973). We searched for all studies that estimated elk vital rates and acquired data from published literature, technical progress

reports and presentations, and via personal communication ($n = 37$ total sources). For survival, we only included sources that estimated annual rates from radiomarking and monitoring of individual elk. We excluded sources that derived calf survival from annual calf:female ratios because this metric is a composite of fecundity and calf survival and may be confounded by changes in female age structure (Bonenfant et al. 2005). We did not account for the heterogeneity in different methods of estimating survival (e.g., proportion of animals surviving time period, Kaplan–Meier survival estimator, and capture–recapture models). We only included sources that estimated annual pregnancy rates of aged Rocky Mountain female elk from uteri examinations or measurement of PSPB. We did not account for different times during gestation when pregnancy status was assessed; however, the majority of these data were derived from examinations of uteri that occurred during late autumn or winter hunting seasons.

For calf survival and the 4 age-specific fecundity rates (yearling, prime-age, old-age, and senescent) we used the grand mean of the age-specific point estimates; therefore, these rates represented averages across broadly different elk populations and habitats. We did not weight means by study-year sample size because they did not differ greatly from unweighted means. Few studies estimated age- or stage-specific female elk survival (exceptions included Kunkel and Pletscher 1999 and Garrott et al. 2003); instead studies often reported survival of "adult, female elk" or simply survival of "cow elk." Therefore, to decompose the female survival point estimates and estimate age-class-specific survival rates, we assumed a generalized survivorship schedule and age structure in these samples based on Houston (1982).

We derived the survivorship structure from Houston's (1982) female-only life-table for the Northern Yellowstone elk in which average prime-age female survival ($\hat{S}_{pa} = 2$–9 yr old) was greatest, and yearlings ($\hat{S}_{yr} = 1$ yr old), old-age females ($\hat{S}_{oa} = 10$–14 yr old), and senescent females ($\hat{S}_{sa} = 15$–20 yr old) survived on average at rates 1.21%, 2.94%, and 19.02% lower than that of prime-age females, respectively (Houston 1982). Thus, we first defined these survival rates to be proportional to $\hat{S}_{pa}$:

$$\hat{S}_{yr} = \hat{S}_{pa} \times 0.9879;$$
$$\hat{S}_{oa} = \hat{S}_{pa} \times 0.9706; \qquad (1)$$
$$\hat{S}_{sa} = \hat{S}_{pa} \times 0.8098.$$

We next assumed an age structure that would typify the unknown age structure of radiocollared "cow elk" in the demographic studies. As a starting point, we assumed an age structure of 13% yearling, 72% prime-age, 10% old-age, and 5% senescent female elk based on the average of the female age distributions from 1951 and 1962–1967 described by Houston (1982). Assuming this age structure and the survivorship schedule in equation 1, we decomposed the reported female survival rate into age-specific survival as:

$$\overline{\overline{S}}_{cow} = (0.13 \times \hat{S}_{yr}) + (0.72 \times \hat{S}_{pa}) + (0.10 \times \hat{S}_{oa})$$
$$+ (0.05 \times \hat{S}_{sa}) \qquad (2)$$

where $\bar{\bar{S}}_{cow}$ denotes the grand mean of the female elk survival point estimates. We then used the age-specific survival estimates derived from equation 2 to parameterize a 15 × 15 transition matrix model and calculated the stable age distribution. We substituted this stable age distribution for Houston's age structure and iteratively reestimated age-specific survival rates until the resultant age-structure and survival rates stabilized. Because decomposing female elk survival in this way assumes a consistent survivorship schedule and stable age structure, deviation from these assumed relationships within study populations represents a source of error in our calculations.

Removing Sampling Variance from Process Variance

Almost all studies included in our data set estimated and presented mean vital rates and reported variability in those rates as total variance, which includes both process and sampling variance (Link and Nichols 1994, Gould and Nichols 1998). Process variance is spatial or temporal variance in vital rates that is attributable to a species' life history, habitat, or population dynamics, whereas sampling variance is additional variance resulting from parameter uncertainty. In LSA (and in any sensitivity analysis), we are interested in how process variance in vital rates alone contributes to variation in λ. Separating sampling from process variance was necessary to estimate the true biological variability inherent in each vital rate.

We used the variance discounting method developed by White (2000) because sampling variance is unlikely to be equal across years, and even less likely to be equal across studies. This method weights different variances in different years, according to the observed within-year sampling variance and the estimated environmental variance (Morris and Doak 2002). To implement the White variance-discounting method, we solved the following equation:

$$ 1 = \frac{1}{n-1} \sum_{t=1}^{n} \left[\frac{\left(\bar{X}_i(t) - \bar{\bar{X}} \right)^2}{V_c(X_i) + V\left(X_i(t)\right)} \right] \quad (3) $$

where X_i is the vital rate of individuals of age class i (either survival rate or pregnancy rate), $\bar{\bar{X}}$ is the grand mean of vital rate i, $V[X_i(t)]$ is the observed variance in vital rate i within year t, and V_c is the unknown environmental (i.e., process) variance. We used MATLAB (Student Version 6.5; Mathworks, Inc, Natick, MA) to implement the white.m code written by Morris and Doak (2002). We modified this algorithm to conduct a search across 100,000 plausible values of V_c to find the best estimate of process variance.

We estimated process variance associated with female elk survival, but we could not directly estimate age-specific process variance given the structure of the available data. We set the prime-age and old-age female survival process variance equal to the process variance calculated from the overall female survival data set; this was a conservative approach because it likely inflated process variance in these reportedly invariant vital rates. Gaillard et al. (1998) reported that across large herbivore species the coefficient of variation was larger in yearling survival (1.43 times greater) and senescent survival (1.89 times greater) than in prime adult female survival. Thus, we approximated yearling and senescent female survival process variances as 1.25 and 1.75 times greater than the female survival process variance, respectively.

Elasticity Analysis and LSA

Analytical elasticities quantify the proportional change in λ resulting from an infinitesimal, one-at-a-time, proportional change in a demographic matrix element, while all other elements are held constant (de Kroon et al. 1986, 2000; Caswell 2000). We calculated analytical elasticities for lower-level vital rates from the demographic matrix of mean vital rates. We modified the MATLAB code limitsens.m (Morris and Doak 2002) to conduct LSA. We calculated λ at stable-age distribution and elasticities for each vital rate within 1,000 replicate matrices generated by independently selecting vital rates from Beta (β) probability distributions (Morris and Doak 2002). The mean and the shape of the vital-rate-specific β-distributions were defined by the mean and process variance estimated for each vital rate. Within the LSA, we calculated mean elasticities and their 95% confidence interval for each vital rate across the matrix replicates, the maximum λ value achievable, and the largest proportional change in λ resulting from the highest estimate recorded for each vital rate across all studies. To provide a comparison to classical elasticity analysis, we regressed each vital rate against λ to estimate the proportion of the total variance in λ attributable to the variance in each vital rate.

Examining the Effects of Reported Vital-Rates Changes on Population Growth Rate

We reexamined 4 case studies (Cole et al. 1997, Singer et al. 1997, Smith and Anderson 1998, Ballard et al. 2000), from peer-reviewed, published sources that documented variation in elk vital rates associated with management actions and environmental conditions to evaluate how the magnitude of these reported changes might impact λ. To do this, we altered calf and cow survival rates in the generalized mean matrix model according to the values reported in these studies and calculated the difference in λ resulting from changing the specific vital rate, and we held other vital rates at their mean values. Our objective was not to provide quantitative predictions about how a management action or climatic event would affect population growth but to illustrate, with empirical examples, the potential influence of these sources of vital-rate variability on population growth rate.

RESULTS

Vital Rate and Process Variance Estimates

The grand mean of annual calf survival ($\bar{\bar{S}}_{ca} = 0.354$, range $= 0.060$–0.720) was considerably lower than that of female survival ($\bar{\bar{S}}_{cow} = 0.873$, range $= 0.640$–0.999); both data sets consisted of a similar number of sources, point estimates, locations, and >1,350 animal years (Table 1). We partitioned age-specific female survival as yearling ($\hat{S}_{yr} =$
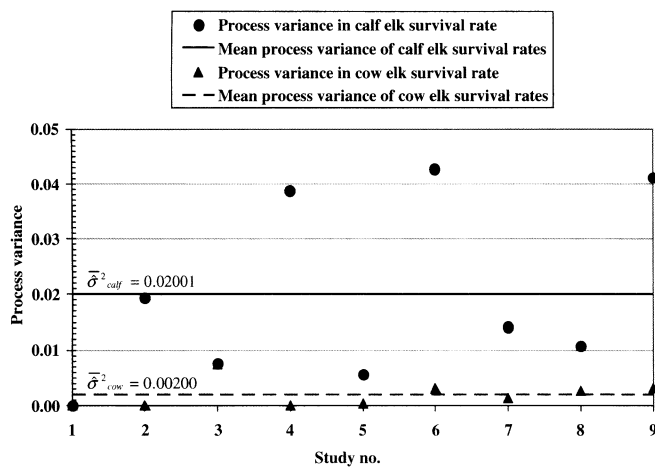
Figure 2. Within study process variance ($\hat{\sigma}^2$) from 9 calf and 9 adult female (cow) elk radiotelemetry-based survival studies and mean process variance of calf and cow survival rates across studies ($\bar{\hat{\sigma}}^2$) conducted across the western United States between 1973–2005. The average number of years or locations was 3.9 and 4.7 in calf and female elk survival studies, respectively. References to the studies are as described in Table 1: 1) 16 and 18; 2) 19 and 22; 3) 20 and 26; 4) 21 and 25; 5) 24 and 32; 6) 27 and 32; 7) 28 and 32; 8) 29 and 35; 9) 34 and 34.

0.883), prime-age ($\hat{S}_{pa} = 0.894$), old-age ($\hat{S}_{oa} = 0.868$), and senescent ($\hat{S}_{sa} = 0.724$), with a stable age-distribution of 12.3%, 61.6%, 17.7%, and 8.4%, respectively. The mean prime-age pregnancy rate ($\bar{\hat{P}}_{pa} = 0.928$, range = 0.781–0.988) was greater than that of yearling ($\bar{\hat{P}}_{yr} = 0.198$, range = 0.000–0.500), old-age ($\bar{\hat{P}}_{oa} = 0.864$, range = 0.750–0.950), and senescent female ($\bar{\hat{P}}_{sa} = 0.530$, range = 0.370–0.692; Table 1) pregnancy rates.

Overall, we found considerable disparity in the process variance of individual vital rates. Process variance in calf survival (0.039) was approximately 11 times greater than process variance in female survival (0.003) across the survival rate data sets (Table 1). Similarly, within-study process variance in calf survival averaged 0.020 (range = 0–0.043) and was approximately 10 times greater than within-study process variance in female survival which averaged 0.002 (range = 0–0.007; Fig. 2). Process variance in yearling (0.015), old-age (0.003), and senescent pregnancy rates (0.006) was approximately 12, 2, and 5 times greater, respectively, than variance in prime-age pregnancy rate (0.001; Table 1). Process variance in female survival was approximately 3 times greater than variance in prime-age female pregnancy rate.

Sensitivity Analysis

Prime-age female survival had the highest elasticity (0.623) among vital rates in the transition matrix of mean rates, followed by yearling survival (0.131), calf survival (0.131), prime-age fecundity (0.097), and old-age female survival (0.092); remaining vital rates had elasticities <0.03 (Fig. 3a). Female survival elasticity (0.869) summed across age classes (yearling, prime-age, old-age, and senescent) was markedly greater than calf survival elasticity (0.131) and fecundity elasticity summed across age classes (0.131). Mean
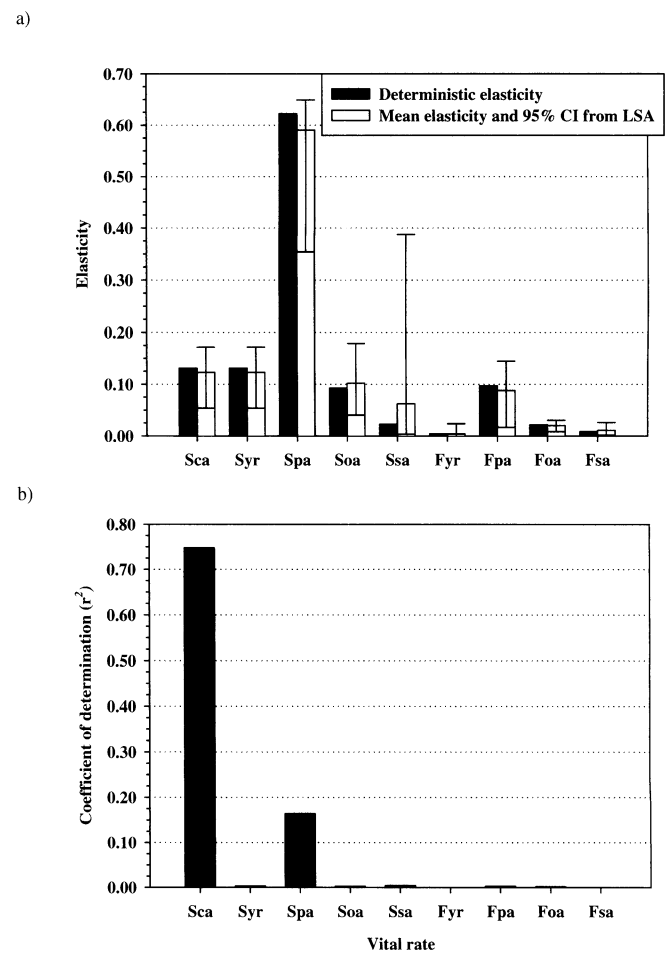

Figure 3. Deterministic elasticities of each elk vital rate calculated from the mean matrix model and mean elasticities and their 95% confidence intervals from the matrix replicates in Life-Stage Simulation Analysis (LSA; a). The variation in population growth rate explained by variation in each vital rate (r^2) in LSA (b). Vital-rate notations are: calf survival (S_{ca}), yearling survival (S_{yr}), prime-age adult survival (S_{pa}), old-age adult survival (S_{oa}), senescent adult survival (S_{sa}), yearling fecundity (F_{yr}), prime-age adult fecundity (F_{pa}), old-age adult fecundity (F_{oa}), and senescent adult fecundity (F_{sa}).

elasticities of the 1,000 matrix replicates ranked vital rates in the same order with the exception of ranking old-age survival higher than prime-age fecundity and yearling fecundity slightly higher than senescent fecundity (Fig. 3a).

The vital rates generated from 1,000 simulated matrix replicates in the LSA represented the process variance present in the age-specific vital-rate data sets (Fig. 4). The mean λ across matrix replicates was 0.980 ± 0.002 (SE) and ranged from 0.726 to 1.217. Variation in calf survival (Fig. 4) explained an overwhelming majority of the variation in λ ($r^2 = 0.748$; Figs. 3b, 5). Prime-age female survival ($r^2 = 0.164$) explained considerably less variation (Fig. 3b). Thus, the main result from the LSA is that the magnitude of variation in calf survival, despite its relatively low elasticity, dramatically influenced population growth rate. The maximum λ value achievable when we set annual calf survival at its highest reported rate (0.720; Smith et al. 1997) and we held all other vital rates at their mean was 1.108; this represented an 11.2% maximum proportional change in λ. The maximum λ value achievable when we set annual
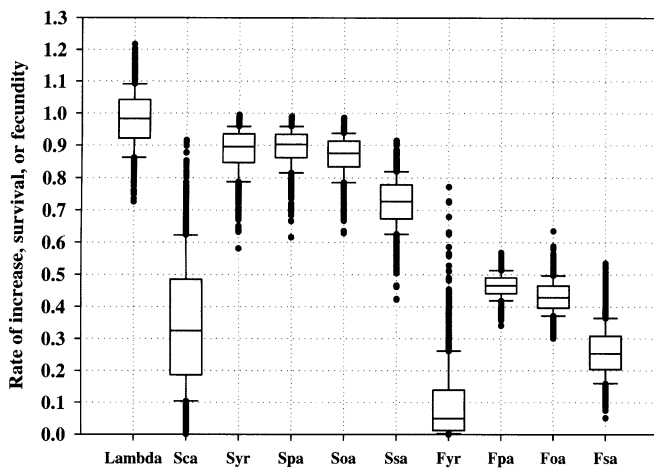
Figure 4. Box plots of the median, percentiles (10th, 25th, 75th, 90th), and outliers for elk population growth rates (λ) and age class-specific vital rates in 1,000 simulated population-matrix model replicates generated in Life-Stage Simulation Analysis. Vital-rate notations are calf survival (S_{ca}), yearling survival (S_{yr}), prime-age adult survival (S_{pa}), old-age adult survival (S_{oa}), senescent adult survival (S_{sa}), yearling fecundity (F_{yr}), prime-age adult fecundity (F_{pa}), old-age adult fecundity (F_{oa}), and senescent adult fecundity (F_{sa}).

prime-age female survival at its highest reported rate (0.999; Unsworth et al. 1993) and we held all other vital rates at their mean was 1.069; this represented a 7.3% maximum proportional change in λ.

Examining the Effects of Reported Vital-Rates Changes on Population Growth Rate

We identified 2 studies (Cole et al. 1997, Ballard et al. 2000) that reported variation in annual adult female elk survival associated with different harvest management approaches. Female survival that was 0.066 higher in hunting areas with limited vehicular access compared to areas with complete vehicular access (Cole et al. 1997) resulted in a 0.063 increase in λ when we included these female survival rates in the mean matrix model (included in yearling, prime, and old-age classes; Fig. 6). Similarly, female survival was 0.072 greater in an unhunted herd versus a hunted herd (Ballard et al. 2000), increasing λ by 0.068 (Fig. 6). Population growth rate was influenced by these relatively small changes in female survival because of the high elasticity of this vital rate ($e_{Scow} = 0.869$ when summed across age classes).

Smith and Anderson (1998) reported variation in calf survival associated with a managed change in winter habitat quality. The winter survival rate of calves that migrated off of the National Elk Refuge (NER), and were not food supplemented, was 0.714, compared to a 0.886 survival rate for those that were fed on the NER. This increase in calf survival translated into a 0.035 positive change in λ when incorporated into our matrix model (Fig. 6). Although food supplementation may be an undesirable management technique in many scenarios, it represented an example of how an immediate increase in winter habitat quality might influence λ when solely operating on calf survival. Singer et al. (1997) reported that calf survival increased by 0.489
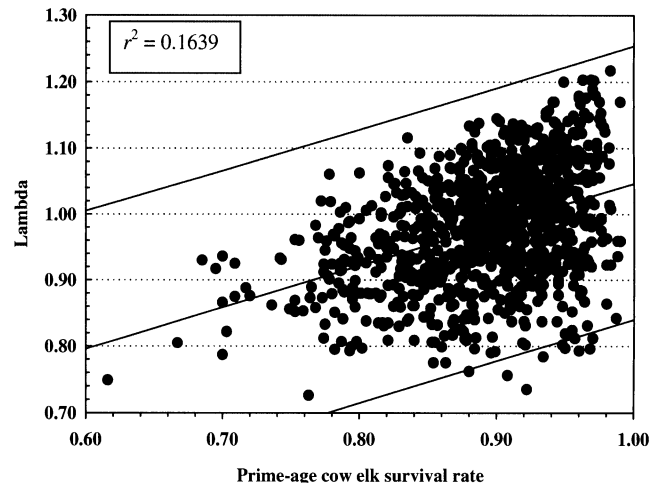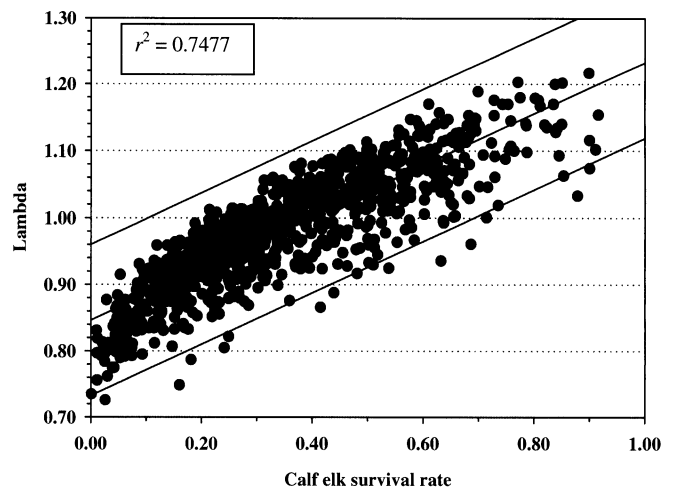

Figure 5. Finite rate of increase (λ) regressed on calf and prime-age female (cow) elk survival rates for 1,000 simulated population matrix model replicates generated in Life-Stage Simulation Analysis (LSA), encompassed by 99% prediction intervals. The coefficient of determination is also presented for each regression. The coefficient of determination represents the variation in the population growth rates explained by the variation in each vital rate in LSA.

following a year with multiple climatic and stochastic environmental effects. The magnitude of the response in calf survival generated a large increase in λ of 0.187 (Fig. 6). We recognize that it is difficult to discern the extent to which variation in these calf elk survival rates are attributable to those primary factors identified by the authors, to other extrinsic factors, or to interactions among factors (e.g., density $\times$ climate; Portier et al. 1998). Modeled changes in λ may also differ from populations that are strongly controlled by density dependence, as our model assumes density-independent population growth. However, these 2 studies suggest that calf survival, given its inherent variability and despite its relatively lower elasticity, can influence λ as much, or more, than adult female survival, the vital rate with the greatest elasticity.

DISCUSSION

We applied the quantitative framework of LSA to couple elasticity measures with empirical estimates of vital-rate
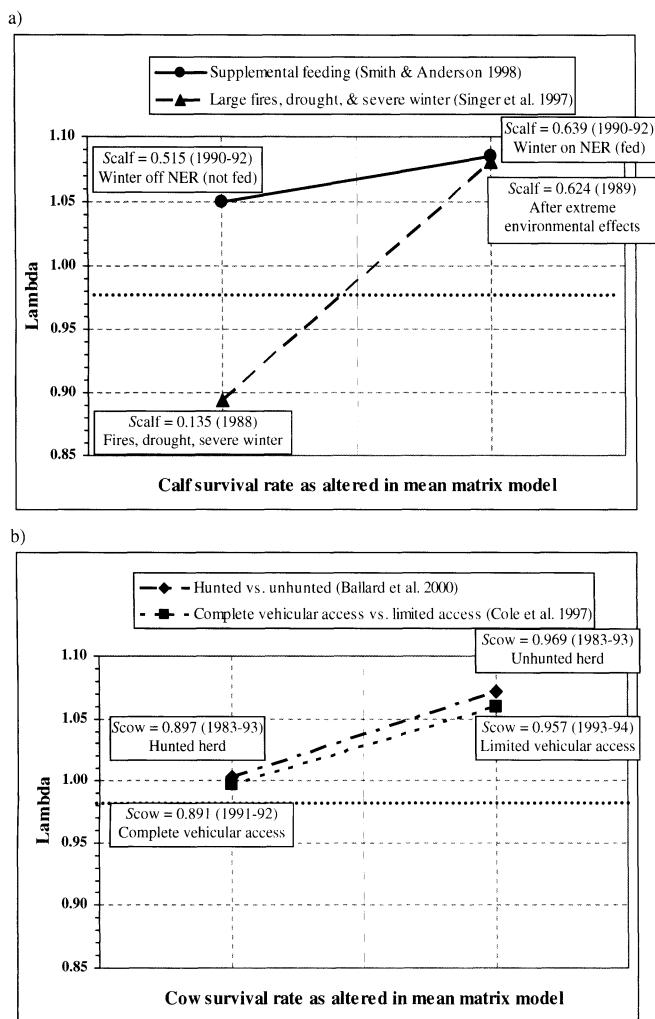
a)

b)

Figure 6. Variation in elk population growth rate (λ) estimated from changing calf (a) or adult female (cow; b) survival rates as reported in 4 published case studies conducted across the western United States between 1983–1994 (other vital rates were held at their x̄ values; Table 1). Vital rate values as altered in the mean matrix model are labeled. The λ value associated with the mean matrix model is denoted (0.980) and the dependent variable scales are equal; therefore, the different slopes represent the change in λ resulting from the various influences on the specific elk vital rate.

variability and assess the realized impact of individual elk vital rates on variability in population growth rates. The majority of the variation reported in elk population growth, both within populations over time and across populations, is likely predominantly driven by variation in calf survival and not by variation in female survival or fecundity rates (Figs. 3b, 5). Calf survival has a greater overall impact on population growth rate compared to that of female survival because of the disproportionate process variances in these vital rates (Table 1). Given the elasticity values derived from our mean matrix model (Fig. 3a), the magnitude of change in calf survival would need to be over 6 times greater than the magnitude of change in female survival to have an equivalent influence on λ. This outcome is not only possible, but highly probable, given that process variance in calf survival was, on average, an order of magnitude higher than process variance in female survival (Fig. 2). Gaillard et al. (1998, 2000) showed that this pattern of invariable adult

survival coupled with highly variable calf survival is consistent across most ungulate taxa, suggesting that calf survival governs population dynamics. Our work demonstrates that calf elk survival can explain as much as 4 times more of the variation in λ than variation in adult survival (Fig. 5). In contrast, variation in adult survival was shown to be largely responsible for population fluctuations of African ungulates in Kruger National Park, implying that the pattern of constant adult survival may not be generalizable to ungulate populations in tropical regions (Owen-Smith and Mason 2005).

The pattern in adult female elk survival of high elasticity coupled with low process variance is consistent with the inverse relationship between elasticity and temporal variance in life-history traits demonstrated by Pfister (1998) across an array of taxa. Because environmental variability negatively influences the stochastic population growth rate, natural selection should minimize variation in vital rates that have high elasticity (Pfister 1998). Adult females are capable of influencing their survival rate by making reproductive or behavioral trade-offs (Albon et al. 1983), which may dampen temporal variation in female survival. Gaillard and Yoccoz (2003) have shown that adult survival in ungulates appears to be canalized against such temporal variability. However, because a broad range of anthropogenic stressors influence modern wildlife populations, high variability (across space or time) in a vital rate should not be used to infer that it has a negligible influence on λ. Indeed, populations may rapidly decline when anthropogenic effects negatively impact a vital rate selected to have high elasticity and express low variation, as was the case with elk at the turn of the 20th century (under intense hunting pressure) and more recently in loggerhead sea turtle (*Caretta caretta*; Crouse et al. 1987) and northern spotted owl (*Strix occidentalis caurina*; Noon and Biles 1990) populations.

Adult and yearling pregnancy rates had very little influence on λ, given their elasticity and variability patterns. Declining elk recruitment may be partly attributable to depressed pregnancy rates (Cook et al. 2004, Raithel 2005); however, reductions in elk density and increases in habitat quality will likely only have a significant impact on λ if they improve calf survival. Increases in pregnancy rates without concurrent increases in calf survival are unlikely to reverse those elk populations declining in the northwestern United States.

MANAGEMENT IMPLICATIONS

Annual variation documented in late-winter and spring elk surveys likely results primarily from variation in calf survival over the previous year and to a lesser extent by variation in the realized female harvest of the preceding autumn. The variation in λ attributable to variability in calf survival resulting from stochastic events (such as harsh winters [Singer et al. 1997, Smith and Anderson 1998], adverse spring conditions [Taper and Gogan 2002, Raithel 2005], and large-scale disturbance [Singer et al. 1997]) can be as great, or greater, than the variation in λ resulting from harvest effects on female elk survival. Recognizing the link

between climate, calf survival, and elk population growth may be particularly important in assessing risk in adaptive harvest-management plans. For example, following a harsh winter or a severely cold, dry spring, both of which are likely to considerably impact calf survival, harvest quotas might need to be adjusted downward to achieve population size objectives in the ensuing year. In scenarios where the goal is to increase elk population size, and female survival is already near its biological maximum, managing for increased calf survival may be the most effective target in influencing population growth. When the management objective is to reduce population size, and female harvest is ineffective due to private land refuges that do not permit public elk hunting (Burcham et al. 1999), decreasing calf survival may be an alternative strategy to lower λ. We also note that the most efficient management strategy will not only be determined by the influence of calf survival on λ and the magnitude of change in calf survival due to the management action but also by the cost of the management technique (see Nichols and Hines 2002 for a mathematical description of this idea).

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