

# Inferences About Ungulate Population Dynamics Derived From Age Ratios

NYEEMA C. HARRIS,<sup>1,2</sup> *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA*

MATTHEW J. KAUFFMAN, *United States Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, University of Wyoming, Laramie, WY 82071, USA*

L. SCOTT MILLS, *Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, University of Montana, Missoula, MT 59812, USA*

**ABSTRACT** Age ratios (e.g., calf:cow for elk and fawn:doe for deer) are used regularly to monitor ungulate populations. However, it remains unclear what inferences are appropriate from this index because multiple vital rate changes can influence the observed ratio. We used modeling based on elk (*Cervus elaphus*) life-history to evaluate both how age ratios are influenced by stage-specific fecundity and survival and how well age ratios track population dynamics. Although all vital rates have the potential to influence calf:adult female ratios (i.e., calf:cow ratios), calf survival explained the vast majority of variation in calf:adult female ratios due to its temporal variation compared to other vital rates. Calf:adult female ratios were positively correlated with population growth rate ( $\lambda$ ) and often successfully indicated population trajectories. However, calf:adult female ratios performed poorly at detecting imposed declines in calf survival, suggesting that only the most severe declines would be rapidly detected. Our analyses clarify that managers can use accurate, unbiased age ratios to monitor arguably the most important components contributing to sustainable ungulate populations, survival rate of young and  $\lambda$ . However, age ratios are not useful for detecting gradual declines in survival of young or making inferences about fecundity or adult survival in ungulate populations. Therefore, age ratios coupled with independent estimates of population growth or population size are necessary to monitor ungulate population demography and dynamics closely through time. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1143–1151; 2008)

DOI: 10.2193/2007-277

**KEY WORDS** age ratios, *Cervus elaphus*, elk, indices, life-stage simulation analysis, monitoring, population growth rate, recruitment, sensitivity analysis, survival, ungulate.

Age ratios are indices regularly incorporated into many wildlife-monitoring programs. For example, age ratios are used to monitor age structure and recruitment, survival, and reproductive rates in birds and marine mammals (Miller and Hatfield 1974, de la Mare 1990, Tanaka 1990, Menu et al. 2002, Iverson et al. 2004, Rohwer 2004). Age ratios such as calf:cow or fawn:doe ratios are collected regularly from ungulate populations during herd composition surveys and are widely utilized to infer demographic trends. (Note: calf:ad F and fawn:ad F are used hereafter in place of the traditional calf:cow and fawn:doe, respectively.) Ungulate age ratios are used to estimate fecundity and survival rate of young in harvested, threatened, and endangered populations (White et al. 1996, Unsworth et al. 1999, Kinley and Apps 2001, Bright and Hervert 2005, Wittmer et al. 2005). Most commonly, age ratios index recruitment, which is the product of fecundity and survival of young (White and Garrott 2005).

Changes in age ratios are also presumed to assist in evaluating how perturbations affect ungulate populations. Commonly, state wildlife agencies use age ratios to infer effects of hunter harvest on ungulates or to quantify impacts of predators such as wolves (*Canis lupus*) on elk (*Cervus elaphus*) and caribou (*Rangifer tarandus*) calf mortality (Valkenburg et al. 2004, White and Garrott 2005). Other perturbations assessed by age ratios include disease on

bighorn sheep (*Ovis canadensis*) demography, scarcity of forage on caribou calf production, high densities on elk populations, and winter severity on elk calf survival (Post and Klein 1999, Monello et al. 2001, Taper and Gogan 2002, Garrott et al. 2003).

Despite common and wide use in ungulate research and management, many authors have questioned the validity of using age ratios to monitor populations (Caughley 1974, McCullough 1994). The primary criticism is that the index itself is a ratio. The numerator represents the number of surviving young and the denominator represents the number of yearling and adult females. Over 30 years ago, Caughley (1974) argued that age ratios could be misleading because they cannot reveal dynamics of the individual components in the ratio. Caughley (1974) demonstrated that dramatic changes in population sizes can go unmarked by age ratios and different mechanisms in increasing and decreasing populations may yield the same trend in age ratios. Similarly, McCullough (1994) emphasized the need to understand assumptions and limitations of age ratios when applied to ungulate management, particularly using mature females as the reference class in the denominator. McCullough (1994) argued that the reference class must be constant and that depicting ratios as the number of young per female masked variability in mature female survival caused by changes in density, weather, predator pressure, harvest regimes, or forage quality.

Despite these cautionary notes, it remains unclear what demographic trends age ratios accurately index and what power they have to detect important perturbations. These

<sup>1</sup> E-mail: ncharris@ncsu.edu

<sup>2</sup> Present address: Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC 27695, USA

**Table 1.** Female-based, prebirth pulse, Leslie matrix representing the elk life-history model.<sup>a</sup>

0	$F_{yr} S_{ca}$	$F_{pa} S_{ca}$	$F_{oa} S_{ca}$	$F_{sa} S_{ca}$	$F_{pa} S_{ca}$	$F_{oa} S_{ca}$	$F_{oa} S_{ca}$	$F_{oa} S_{ca}$	$F_{oa} S_{ca}$	$F_{sa} S_{ca}$					
$S_{yr}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	$S_{pa}$	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	$S_{pa}$	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	$S_{pa}$	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	$S_{pa}$	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	$S_{pa}$	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	$S_{pa}$	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	$S_{pa}$	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	$S_{pa}$	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	$S_{pa}$	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	$S_{oa}$	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	$S_{oa}$	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	$S_{oa}$	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	$S_{sa}$	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	$S_{sa}$	0

<sup>a</sup> Notation of the vital rates is as follows: survival calves ( $S_{ca}$ ), survival yearlings ( $S_{yr}$ ), survival prime-age ad ( $S_{pa}$ ), survival old-age ad ( $S_{oa}$ ), survival senescent ad ( $S_{sa}$ ), fecundity yearlings ( $F_{yr}$ ), fecundity prime-age ad ( $F_{pa}$ ), fecundity old-age ad ( $F_{oa}$ ), and fecundity senescent ad ( $F_{sa}$ ). We assumed a 50:50 calf sex ratio at the prebirth census and used reported pregnancy rates as a surrogate to fecundity. We parameterized the matrix using vital rates presented by Singer et al. 1997, Garrott et al. 2003, and White and Garrott 2005. The projection interval of the matrix is 1 yr.

uncertainties remain because we lack a quantitative understanding of what observed changes in age ratios actually represent in terms of population dynamics. Specifically, we do not know how age ratios respond to changes in vital rates that comprise their individual components, nor do we know what degree of natural variability we should expect to observe in age ratios, or how variation in vital rates compromises the ability of age ratios to detect directional changes in vital rates or population growth rate ( $\lambda$ ). These uncertainties are particularly problematic in the face of growing concerns about recruitment, survival of young, and fecundity that have recently arisen because of reported declines in age ratios in many ungulate populations including elk (Noyes et al. 1996), mule deer (*Odocoileus hemionus*; White et al. 2001), and caribou (Post and Klein 1999).

Our objectives were to connect age ratios to changes in vital rates and population growth and to identify which inferences are appropriate when trends in these indices are observed (assuming age ratios obtained are precise and unbiased). Specifically, we estimated the relative importance of individual vital rates on ungulate age ratios by examining the deterministic and stochastic influence of vital rate variation on predicted age ratios. We also assessed the ability of age ratios to index population dynamics and to identify deterministic decreases in the survival of young. We conducted our analyses using calf:adult female ratios and chose elk as our model species because they are widespread, abundant, well-studied, and highly managed.

## METHODS

We constructed a  $15 \times 15$  prebirth pulse, female-based matrix for elk based on their life history (Table 1). Age classes consisted of calves, yearlings (1 yr old) and prime-age adults (2–9 yr old), old-age adults (10–13 yr old), and senescent adults ( $\geq 14$  yr old). We used vital rates from a

long-term demographic study in Yellowstone National Park (YNP), USA, to parameterize yearling and prime-age survival, old-age survival, yearling pregnancy, prime-age pregnancy, and old-age pregnancy (Garrott et al. 2003). We set both yearling survival and old-age pregnancy rates to equal those of prime-age adults because yearlings and old-age individuals are often pooled with prime-age females (Noyes et al. 1996, Gaillard et al. 2000, Garrott et al. 2003); in addition, Garrott et al. (2003) found no evidence of reproductive senescence between prime-age and old-age elk. We obtained an estimate of calf survival and senescent pregnancy rate from other studies conducted in YNP (Singer et al. 1997, White and Garrott 2005). Elements in the top row of the matrix included both calf survival and fecundity. Fecundity, the number of female calves per female assuming a 50:50 sex ratio, was solely a function of pregnancy rate because intrauterine mortality is negligible in free-ranging elk and multiple births are rare ( $< 1.0\%$ ; Houston 1982). We also estimated senescent survival as a fraction of old-age survival following Raithel et al. (2007) because dramatic declines in survival of older age classes have been detected in other ungulate species (Gaillard et al. 2000).

We estimated all calf:adult female ratios in our study as the number of calves (doubled to account for our F-only matrix) divided by number of yearlings and adults. We employed 2 methods to determine the relative importance of each vital rate on calf:adult female ratios. First, in a deterministic analysis, we constructed a mean matrix with invariant vital rates and independently imposed an arbitrary 10% change in each vital rate, while all other vital rates were held constant. We assessed the relative importance of vital rates by quantifying proportional changes in calf:adult female ratios at stable age distribution (SAD) that resulted from this manual perturbation for each vital rate. Second, we used a variant of life-stage simulation analysis (Wisdom and Mills 1997, Wisdom et al. 2000) to assess how natural patterns of

vital-rate variability influenced calf:adult female ratios. We incorporated variation in vital rates from Singer et al. (1997) and Garrott et al. (2003), which are consistent with how ungulate vital rates vary in nature (Gaillard et al. 2000). We obtained the calf:adult female ratios at SAD from 1,000 replicate matrices generated by independent selections of fecundity rates from stretched Beta ( $\beta$ ) probability distributions (ranging 0.0–0.5) and survival rates from Beta ( $\beta$ ) probability distributions (ranging 0.0–1.0; Table 2). We report coefficients of determination for each vital rate, which estimates the proportion of total variation in the calf:adult female ratio attributed to variation in each vital rate.

We assessed the ability of calf:adult female ratios to track changes in vital rates and  $\lambda$ , using stochastic projections that incorporated transient dynamics, which allowed us to determine what extractable information calf:adult female ratios provide when they are monitored routinely over time. We specified a starting population size ( $N$ ) vector of 1,000 individuals at SAD and multiplied that vector by a matrix to create a new population vector. We generated each matrix by a random selection of vital rates within their specified distributions that were bounded by values corresponding to natural patterns of variability (see previous section). We obtained calf:adult female ratios from each new population size vector during 100 replicate projections of 50 time steps each. We used a projection interval of 1 year, which made calf:adult female ratios equivalent to those obtained during annual spring surveys. We assessed the ability of calf:adult female ratios to track changes by regressing calf:adult female ratio at time  $t+1$  on the vital rate at time  $t$  (or on  $\lambda$ , where  $\lambda = N_{t+1}/N_t$ ), and report coefficients of determination between each vital rate and calf:adult female ratio. We also report graphically the proportion of time steps from 1,000 projections where calf:adult female ratios correspond to decreasing ( $\lambda \leq 0.994$ ), stationary ( $0.995 \leq \lambda \leq 1.004$ ), and increasing ( $\lambda \geq 1.005$ ) populations.

We included negative density-dependence into stochastic projections to account for changes in certain vital rates as population size approaches carrying capacity. We expected calf survival and cow pregnancy rate to be more sensitive to density than other vital rates in our matrix (Eberhardt 1977, Fowler 1987, Milner et al. 1999, Varley and Boyce 2006). Although empirical estimates of density-dependence for elk are limited, Singer et al. (1997) reported calf survival at varying population sizes and Stewart et al. (2005) measured the response of cow pregnancy from experimental manipulations of density. We fit the Ricker function of negative density-dependence using data from Singer et al. (1997) and Stewart et al. (2005) following Morris and Doak (2002) as

$$VR[E(t)] = VR(0)^{-\beta E(t)}$$

where the vital rate ( $VR =$  calf survival or F fecundity) is a function of current density  $[E(t)]$ , and  $VR(0)$  is the vital rate when density is close to zero. The fitted parameter,  $\beta$ , represents the negative response of the vital rates to increasing density and was calculated from the empirical

calf survival and pregnancy studies as the slope in a linear regression of the log vital rate against density.

We also evaluated the ability of calf:adult female ratios to detect changes in calf survival across a range of perturbation scenarios, using our stochastic projections. We focused specifically on calf survival because of its importance to population growth due to its temporal variation and close correspondence with the calf:adult female ratios (Gaillard et al. 1998, 2000; Raithel et al. 2007). We allowed all vital rates to vary independently around a constant mean. However, for calf survival, we set the mean survival rate to 0.60 for 5 years before instigating a 5–50% annual decline in survival. We maintained a constant annual coefficient of variation in all model runs by adjusting variance around the mean calf survival rate to assure variance estimates remained consistent with empirical data and to allow for direct comparison between simulations. We replicated each scenario 50 times and projected populations for  $\leq 15$  years. All vital rates were density-independent for these perturbations. These annual declines in calf survival simulate a gradient in perturbations that might occur in nature, ranging from gradual declines in habitat quality (or increasing predators, etc.) to extreme environmental events. We evaluated whether a decline was detected by regressing the calf:adult female ratio against time. We tested whether the slope differed significantly from zero using  $\alpha < 0.10$  to maximize the power to detect a change in cow:adult female ratio as calf survival is decreased.

## RESULTS

### Vital Rate Influence on Calf:Adult Female Ratios

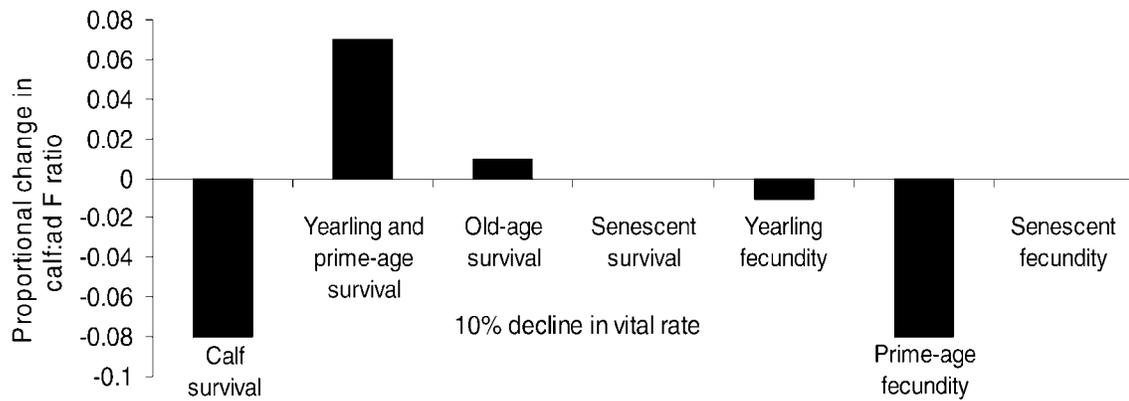
The potential effect of changes in vital rates on calf:adult female ratios were not equal across vital rates. In the deterministic analysis, substantial proportional changes in calf:adult female ratios resulted from modeled 10% changes in calf survival, prime-age survival, and prime-age fecundity (Fig. 1A). Not surprisingly, these vital rates changed calf:adult female ratios in different directions. Decreasing yearling and prime-age (1–9 yr old) survival influenced the denominator of calf:adult female ratios causing the ratio to increase. In contrast, a decline in calf survival and prime-age fecundity in the numerator caused calf:adult female ratios to decrease.

Vital rates varied by different amounts in our simulations (and in nature) and this led to disparate impacts on calf:adult female ratios. Calf survival was the most variable vital rate and this variation explained nearly all the variation in calf:adult female ratios at stable age distribution ( $r^2 = 0.96$ ; Fig. 1B). Prime-age fecundity ( $r^2 = 0.012$ ) and yearling fecundity ( $r^2 = 0.009$ ) explained most of the remaining variation in the calf:adult female ratio. Adult survival had a negligible influence on the variation in calf:adult female ratios ( $r^2 = 0.002$ ) because it was invariable compared to other vital rates.

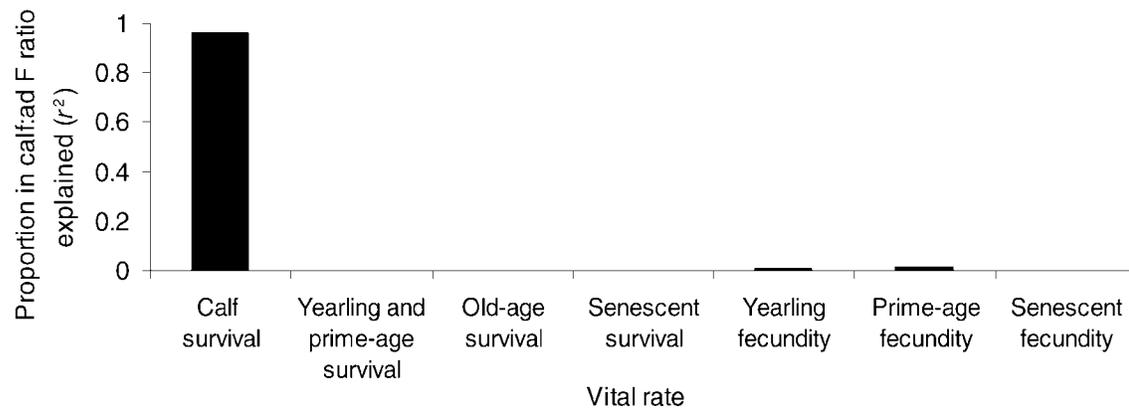
### Calf:Adult Female Ratios as an Index of Population Dynamics

The ability of calf:adult female ratios to reflect changes in vital rates from year to year was not consistent among vital

A)



B)



**Figure 1.** Sensitivity analysis of calf:adult female ratios for elk at stable age distribution. (A) Proportional change in calf:adult female ratios from a 10% decline in each vital rate from the deterministic modeling. (B) Variation in calf:adult female ratio explained ( $r^2$ ) by natural variability in each vital rate from 1,000 replicate matrices in the life-stage simulation analysis.

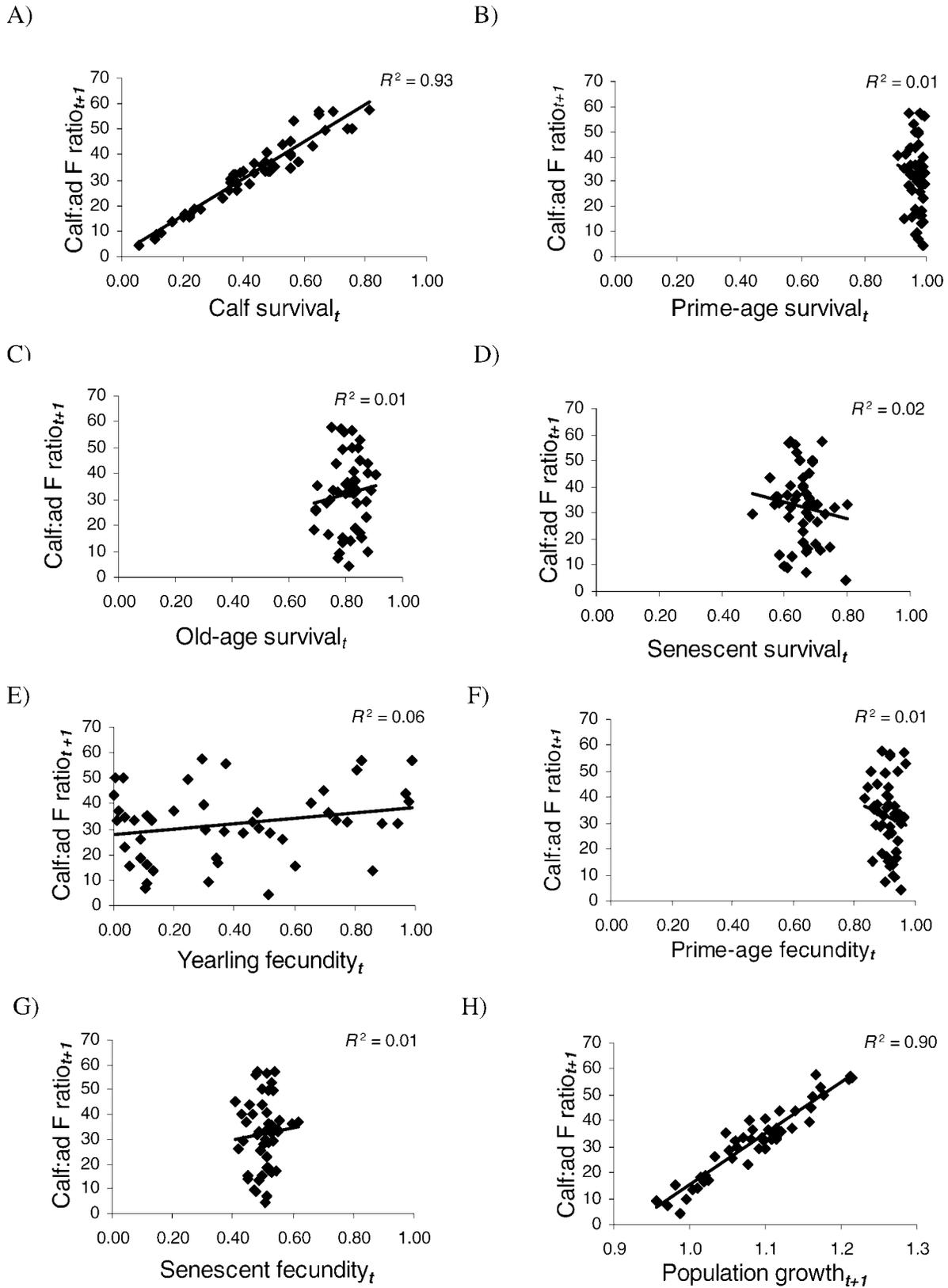
rates (Fig. 2). Calf:adult female ratios were strongly correlated with calf survival the previous year in projection models (Fig. 2A; from 100 simulations: mean  $r^2 = 0.94$ , SD in  $r^2 = 0.01$ ). Calf:adult female ratios also showed a weak relationship to changes in yearling fecundity in the previous year (Fig 2E; mean  $r^2 = 0.03$ , SD = 0.05). The remaining vital rates had a negligible influence on calf:adult female ratios due to their narrow range of variation ( $S_{pa}$ :  $r^2 = 0.02$ , SD = 0.03;  $S_{oa}$ :  $r^2 = 0.02$ , SD = 0.03;  $S_{sn}$ :  $r^2 = 0.02$ , SD = 0.03;  $F_{pa}$ :  $r^2 = 0.03$ , SD = 0.04;  $F_{sn}$ :  $r^2 = 0.02$ , SD = 0.02 [variables defined in Table 1]). There were no qualitative differences between the density-independent and density-dependent models in the response of calf: adult female ratios to changes in vital rates.

Calf:adult female ratios were positively correlated with estimates of annual  $\lambda$  (Fig. 2H, mean  $r^2 = 0.89$ ; SD = 0.03) and were reasonably successful in distinguishing among increasing, stationary, and decreasing populations (Fig. 3). When calf:adult female ratios were  $>20:100$  ( $>28:100$

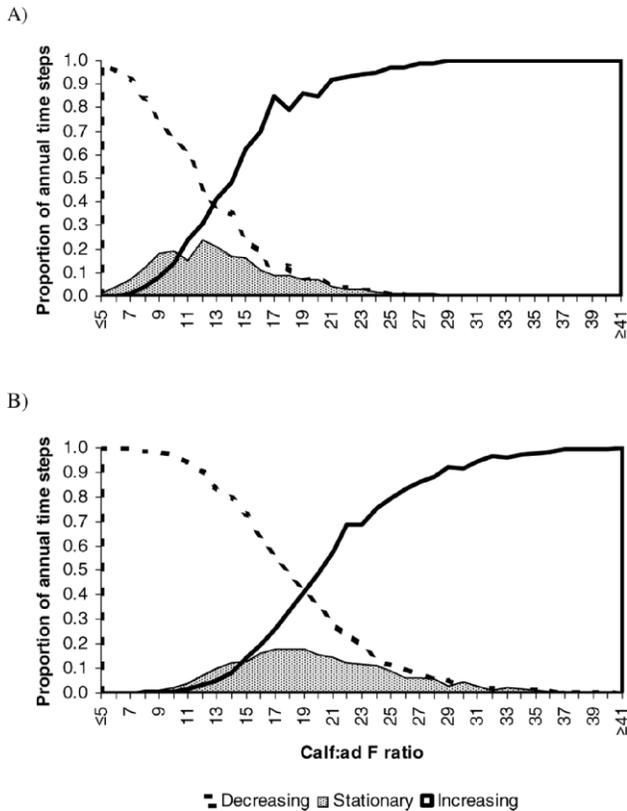
under density-dependence) there was a  $\geq 90\%$  chance that the population was increasing; conversely, calf:adult female ratios  $<8:100$  ( $<12:100$  under density-dependence) were virtually certain to indicate a decreasing population, given the vital rates and their associated modeled variances. However, there was a high level of ambiguity in the trajectory of the population when calf:adult female ratios were between about 12–16:100 for density-independent

**Table 2.** Minimum, maximum, and mean values of elk vital rates from 1,000 matrix replicates in life-stage simulation analysis.

Vital rate	Min.	Max.	$\bar{x}$
Calf survival rate	0.039	0.931	0.431
Yearling and prime-age survival rate	0.867	0.998	0.969
Old-age survival rate	0.564	0.943	0.788
Senescent survival rate	0.443	0.838	0.663
Yearling fecundity rate	0.000	0.499	0.199
Prime-age and old-age fecundity rate	0.372	0.498	0.455
Senescent fecundity rate	0.181	0.312	0.249



**Figure 2.** Ability of elk calf:adult female ratios to reflect changes in A) calf survival, B) prime-age survival, C) old-age survival, D) senescent survival, E) yearling fecundity, F) prime-age fecundity, G) senescent fecundity, and H) population growth ( $\lambda$ ). Stochastic projections were density-independent with 1-year time intervals projected 50 years. Results are shown for a single, representative 50-year projection. The mean coefficient of determination and standard deviation values across 100 simulations are given in text.



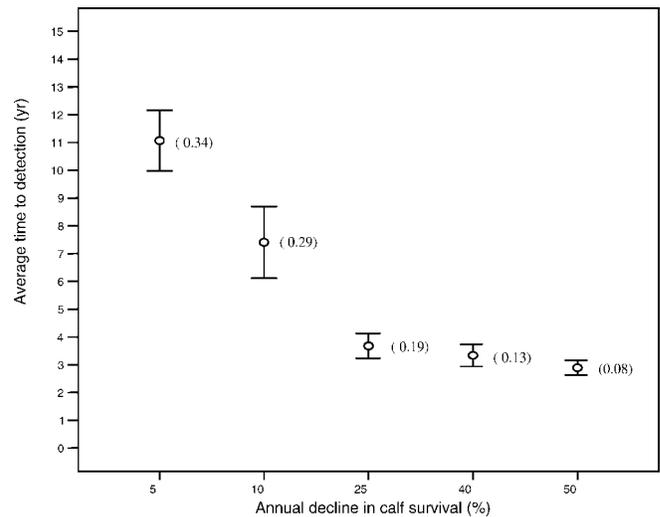
**Figure 3.** Distribution of calf:adult female ratios corresponding to decreasing ( $\lambda \leq 0.994$ ), stationary ( $0.995 \leq \lambda \leq 1.004$ ) and increasing ( $\lambda \geq 1.005$ ) populations from A) density-independent, and B) density-dependent (incorporated in calf survival and fecundity vital rates) stochastic projections for elk. Models were projected 50 years with 1-year time intervals and 1,000 replications.

models and 17–23:100 for density-dependence models. For example, with a calf:adult female ratio of 20:100 and density-dependence operating, there was a 36%, 16%, and 48% chance that the population was decreasing, stationary, or increasing, respectively. In all cases, calf:adult female ratio thresholds important for management are slightly different for populations experiencing density-dependence.

The ability of calf:adult female ratios to detect actual declines in calf survival varied depending on the severity of perturbations in density-independent models (Fig. 4). Small perturbations in calf survival, such as 5% annual declines, were detected by the calf:adult female ratios in 62% (31/50) of replicates. However, these small perturbations in calf survival took on average 11 years to detect. Calf:adult female ratios detected 50% annual declines in calf survival in 94% (47/50) of replicates within a 3-year period, but by this time mean calf survival had dropped to 0.08 (Fig. 4).

## DISCUSSION

Our analyses demonstrated that age ratios can be changed by several vital rates, with the direction of the change dependent on whether the vital rate influences the numerator or denominator and the magnitude of change dependent on the degree of variability in the vital rate. Calf survival has the greatest influence on the age ratio because it



**Figure 4.** Ability of calf:adult female ratios to detect annual declines in calf survival in elk of varying severities from stochastic projections with 50 replications. Average time to detection in years after perturbation was enforced is given with corresponding 95% confidence intervals. Mean calf survival rate corresponding to average time to detection is presented in the parentheses.

is the most variable vital rate in northern ungulates (Gaillard et al. 1998, 2000; Raithel et al. 2007). For example, juvenile survival ranged from 0.07 to 0.41, whereas adult survival ranged from 0.74 to 0.76 in a mule deer population on Vancouver Island, British Columbia, Canada (Hatter and Janz 1994). The relative stability of adult survival in ungulates indicates that not only is the number of females an appropriate denominator, but also that adult survival does not mask the influence of juvenile survival on age ratios. Therefore, contrary to Caughley (1974) and McCullough (1994), we suggest that age ratios can meaningfully reflect dynamics of an individual component of the ratio, specifically survival of young.

On the other hand, age ratios were a poor index of fecundity in ungulate populations because they did not reflect changes in fecundity of any stage class in our analyses. Similarly, Andelt et al. (2004) concluded that low pregnancy rates could not explain low fawn:adult female ratios in mule deer. Factors that cause changes in pregnancy rate such as male age in elk are also unlikely to explain variation observed in age ratios (Noyes et al. 1996). Yearling fecundity is the second most variable vital rate, but it has little influence on age ratios because it only affects one stage class that represents only a small portion of the population (Raithel et al. 2007). Fecundity of other stage classes is generally high and relatively constant, but is sensitive to density, weather, and habitat quality (Fowler 1987, Gaillard et al. 2000). Our results imply that it is not appropriate to monitor fecundity for any stage through age ratios.

Managers are not only interested in monitoring production and survival of young but also population size and growth. We would not expect a relationship between absolute population size and age ratios based on first principles and previous studies (Coughenour and Singer

1996, Smith and Anderson 1998, Bender and Weisenberger 2005). However, age ratios did positively correlate to estimates of annual  $\lambda$  in our simulations. Gaillard et al. (1998, 2000) and Raithel et al. (2007) have made clear that variation in survival of young drives ungulate population growth. Our results corroborate this general trend for elk and indicate that age ratios are a good index of relative annual changes in  $\lambda$  because they track variation in the most important demographic parameter, survival of young.

The specific calf:adult female ratios associated with increasing ( $\lambda \geq 1.005$ ), stationary ( $0.995 \leq \lambda \leq 1.004$ ), and decreasing ( $\lambda \leq 0.994$ ) populations depended on whether density-dependence was acting on calf survival and fecundity rates (Fig. 3). In an increasing population, calf survival (and therefore calf:ad F ratios) must be higher when density-dependence is occurring. It is probably reasonable to assume newly established, translocated, or highly managed populations are not experiencing density-dependence (e.g., reintroduced Kentucky Elk Herd; Larkin et al. 2003), although vital rates might be depressed by density-dependence in growing, unharvested populations (e.g., Northern Yellowstone Elk Herd; Taper and Gogan 2002). Whether or not density-dependence is occurring, the greatest uncertainty is distinguishing stationary populations from decreasing or increasing populations, an area where uncertainty may not be tolerable depending on management objectives.

Despite strong correspondence between age ratios and calf survival, age ratios did a rather poor job of detecting annual declines in calf survival in the stochastic projections. Only the most severe deterministic declines in calf survival will yield discernable trends in calf:adult female ratios. Most declines in calf survival that are slight and long-lasting will likely go unnoticed if relying solely on age ratios because calf survival varies widely from year to year due to stochastic environmental variation. Lack of detection of slight, long-lasting declines in calf survival is not due to the inability of calf:adult female ratios to track annual variation in calf survival (as evidenced by Fig. 2A). In other words, declines in calf survival that may occur from directional influences (e.g., steadily increasing predator densities) can easily be eroded by the random occurrence of summer droughts and severe winters that strongly control calf survival.

Our conclusions are robust to different mean vital rate estimates, but patterns of variability incorporated in our analyses drove many of our results. We obtained all vital rates and associated estimates of variance from a YNP elk population that was exposed to predation from a suite of predators including grizzly bears (*Ursus arctos horribilis*) and gray wolves instead of human-caused hunting-related mortality. Mean adult survival and its variance from the YNP vital rates were higher ( $\bar{x} = 0.97$ ,  $SE = 0.02$ ) in comparison to a harvested elk population in Arizona ( $\bar{x} = 0.90$ ,  $SE = 0.001$ ; Ballard et al. 2000). Therefore, the variability in adult survival incorporated is a pessimistic estimate and lower values would have an even lesser effect on calf:adult female ratios. In addition, a metaanalysis of elk

demography by Raithel et al. (2007) indicates that patterns of vital rate variability for YNP elk are consistent with other free-ranging elk populations across the United States. We obtained calf survival estimates from Singer et al. (1997), which included a year where calf survival declined by  $\geq 70\%$  due to drought and the 1988 Yellowstone fires. This catastrophic event may have inflated variance around the calf survival estimate in our simulations relative to other elk populations, but it still reflects the predominant pattern of variation of ungulate populations with juvenile survival and yearling fecundity being more variable than adult survival (Gaillard et al. 2000, Raithel et al. 2007). In addition, adult survival is expected to be relatively stable because of its high contribution (elasticity) to  $\lambda$  (Pfister 1998, Gaillard and Yoccoz 2003).

Estimated age ratios are subject to additional sources of variation not incorporated into our simulated environment. Many authors have discussed biases in age ratios recorded in the field due to sightability (Samuel et al. 1987), survey design (Caughley 1977, Gasaway et al. 1985, Samuel et al. 1992), temporal variation in age ratios (McCullough 1993, Bonenfant et al. 2005), observation error (Smith and McDonald 2002, Bender et al. 2003), and behavioral patterns of different age classes (Kaji et al. 2005). Variation observed in age ratios could be attributed mistakenly to changes in survival of young when, in fact, variation could be due to various sources of estimation error. We predicate our relative optimism regarding the utility of age ratios to monitor ungulate population demography and dynamics entirely on estimated ratios being both precise and unbiased.

We believe our results could extrapolate to other North American ungulates, to the extent that life histories and patterns in vital rate variability are similar. However, for other taxa where age ratios are regularly employed to monitor populations—such as birds and marine mammals—differences in life histories and patterns of vital rate variability will mean that individual impacts of vital rates on age ratios may differ from our findings. In addition, there is a continued need to evaluate the relative merits of estimating  $\lambda$  for ungulate populations through vital rates versus age ratios or changes in population size.

## MANAGEMENT IMPLICATIONS

We suggest that age ratios are a valuable component of ungulate monitoring programs. Our analyses demonstrated that calf:adult female ratios are generally predictive of survival of young the previous year and that the directional trend in population growth can often be inferred from age ratio data alone. Also, understanding the role of density-dependence in the monitored ungulate population and minimizing the confounding effects of observation error will help identify the calf:adult female ratios needed to obtain population trajectory objectives. However, the fact that age ratios are unable to discern population trends in the middle range (e.g., 10–20 calves:ad F), and that age ratios may not quickly signal gradual annual declines in survival of young, indicates that age ratios should be coupled with independent

estimates of population growth or population size when close monitoring of ungulate populations is necessary. In conclusion, age ratios are more useful for monitoring survival of young and population growth than evaluating perturbations to ungulate populations.

## ACKNOWLEDGMENTS

We thank D. H. Pletscher, J. W. Thomas, E. Greene, M. J. Thompson, M. J. Kelly, and P. C. Zager for review comments and contributions to this manuscript. We acknowledge Rob and Bessie Welder Wildlife Foundation (contribution no. 670), Montana Cooperative Wildlife Research Unit, Department of Defense Strategic Environmental Research and Development Program, and Safari Club International Foundation for financial contributions to our research. L. S. Mills acknowledges the National Science Foundation (DEB-0415604).

## LITERATURE CITED

- Andelt, W. F., T. M. Pojar, and L. W. Johnson. 2004. Long-term trends in mule deer pregnancy and fetal rates in Colorado. *Journal of Wildlife Management* 68:542–549.
- Ballard, W. B., H. A. Whitlaw, B. F. Wakeling, R. L. Brown, J. C. Devos, Jr., and M. C. Wallace. 2000. Survival of female elk in northern Arizona. *Journal of Wildlife Management* 64:500–504.
- Bender, L. C., W. L. Meyers, and W. R. Gould. 2003. Comparison of helicopter and ground surveys for North American elk *Cervus elaphus* and mule deer *Odocoileus hemionus* population composition. *Wildlife Biology* 9:199–205.
- Bender, L. C., and M. E. Weisenberger. 2005. Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. *Wildlife Society Bulletin* 33:956–964.
- Bonenfant, C., J. Gaillard, F. Klein, and J. Hamann. 2005. Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer *Cervus elaphus* as a model. *Journal of Applied Ecology* 42:361–370.
- Bright, J. L., and J. J. Hervert. 2005. Adult and fawn mortality of Sonoran pronghorn. *Wildlife Society Bulletin* 33:43–50.
- Caughley, G. 1974. Interpretation of age ratios. *Journal of Wildlife Management* 38:557–562.
- Caughley, G. 1977. Sampling in aerial survey. *Journal of Wildlife Management* 41:605–615.
- Coughenour, M. B., and F. J. Singer. 1996. Elk population processes in Yellowstone National Park under the policy of natural regulation. *Ecological Applications* 6:573–593.
- de la Mare, W. K. 1990. Inferring net recruitment rates from changes in demographic parameters: a sensitivity analysis. Report of the International Whaling Commission 40:525–529.
- Eberhardt, L. L. 1977. Optimal management policies for marine mammals. *Wildlife Society Bulletin* 5:162–169.
- Fowler, C. W. 1987. A review of density dependence in populations of large mammals. Pages 401–441 in H. H. Genoways, editor. *Current mammalogy*. Plenum Press, New York, New York, USA.
- Gaillard, J., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13:58–63.
- Gaillard, J., 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.
- Gaillard, J., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306.
- Garrott, R. A., L. L. Eberhardt, P. J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology* 81:33–45.
- Gasaway, W. C., S. D. DuBois, and S. J. Harbo. 1985. Biases in aerial transect surveys for moose during May and June. *Journal of Wildlife Management* 49:777–784.
- Hatter, I. W., and D. W. Janz. 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. *Canadian Journal of Zoology* 72:878–884.
- Houston, D. B. 1982. *The Northern Yellowstone elk: ecology and management*. Macmillan, New York, New York, USA.
- Iverson, S. A., B. D. Smith, and F. Cooke. 2004. Age and sex distributions of wintering surf scoters: implications for the use of age ratios as an index of recruitment. *Condor* 106:252–262.
- Kaji, K., H. Takahashi, J. Tanaka, and Y. Tanaka. 2005. Variation in the herd composition counts of sika deer. *Population Ecology* 47:53–59.
- Kinley, T. A., and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. *Wildlife Society Bulletin* 29:158–164.
- Larkin, J. L., D. S. Maehr, J. J. Cox, D. C. Bolin, and M. W. Wichrowski. 2003. Demographic characteristics of a reintroduced elk population in Kentucky. *Journal of Wildlife Management* 67:467–476.
- McCullough, D. R. 1993. Variation in black-tailed deer herd composition counts. *Journal of Wildlife Management* 57:890–897.
- McCullough, D. R. 1994. What do herd composition counts tell us? *Wildlife Society Bulletin* 22:295–300.
- Menu, S., G. Gauthier, and A. Reed. 2002. Changes in survival rates and population dynamics of greater snow geese over a 30-year period: implications for hunting regulations. *Journal of Applied Ecology* 39:91–102.
- Miller, R. S., and J. P. Hatfield. 1974. Age ratios of sandhill cranes. *Journal of Wildlife Management* 38:234–242.
- Milner, J. M., D. A. Elston, and S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival in Soay sheep. *Journal of Animal Ecology* 68:1235–1247.
- Monello, R. J., D. L. Murray, and E. F. Cassirer. 2001. Ecological correlates of pneumonia epizootics in bighorn sheep herds. *Canadian Journal of Zoology* 79:1423–1432.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer, Sunderland, Massachusetts, USA.
- Noyes, J. H., B. K. Johnson, L. D. Bryant, S. L. Findholt, and J. W. Thomas. 1996. Effects of bull age on conception dates and pregnancy rates of cow elk. *Journal of Wildlife Management* 60:508–517.
- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings from the National Academy of Sciences* 95:213–218.
- Post, E., and D. R. Klein. 1999. Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management* 63:335–345.
- Raithel, R. D., M. J. Kauffman, and D. H. Pletscher. 2007. Impact of spatial and temporal variation in calf survival on the growth of elk populations. *Journal of Wildlife Management* 71:795–803.
- Rohwer, S. 2004. Using age ratios to infer survival and despotic breeding dispersal in hybridizing warblers. *Ecology* 85:423–431.
- Samuel, M. D., E. O. Garton, M. W. Schlegel, and R. G. Carson. 1987. Visibility bias during aerial surveys of elk in north-central Idaho. *Journal of Wildlife Management* 51:622–630.
- Samuel, M. D., R. K. Steinhorst, E. O. Garton, and J. W. Unsworth. 1992. Estimation of wildlife population ratios incorporating survey design and visibility bias. *Journal of Wildlife Management* 56:718–725.
- Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12–25.
- Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson Elk Herd. *Journal of Wildlife Management* 62:1036–1045.
- Smith, B. L., and T. L. McDonald. 2002. Criteria to improve age classification of antlerless elk. *Wildlife Society Bulletin* 30:200–207.
- Stewart, K. M., R. T. Bowyer, B. L. Dick, B. K. Johnson, and J. G. Kie. 2005. Density-dependent effects on physical condition and reproduction in North American elk: an experimental test. *Oecologia* 143:85–93.
- Tanaka, S. 1990. Estimation of natural mortality coefficient of whales from the estimates of abundance and age composition data obtained from

- research catches. Report of the International Whaling Commission 40: 531–536.
- Taper, M. L., and P. J. Gogan. 2002. The Northern Yellowstone elk: density dependence and climatic conditions. *Journal of Wildlife Management* 66:106–122.
- Unsworth, J. W., D. F. Pac, G. C. White, and R. M. Bartmann. 1999. Mule deer survival in Colorado, Idaho, and Montana. *Journal of Wildlife Management* 63:315–326.
- Valkenburg, P., M. E. McNay, and B. W. Dale. 2004. Calf mortality and population growth in the Delta caribou herd after wolf control. *Wildlife Society Bulletin* 32:746–756.
- Varley, N., and M. S. Boyce. 2006. Adaptive management for reintroductions: updating a wolf recovery model for Yellowstone National Park. *Ecological Modelling* 193:315–339.
- White, G. C., D. J. Freddy, R. B. Gill, and J. H. Ellenberger. 2001. Effect of adult sex ratio on mule deer and elk productivity in Colorado. *Journal of Wildlife Management* 65:543–551.
- White, G. C., A. F. Reeve, F. G. Lindzey, and K. P. Burnham. 1996. Estimation of mule deer winter mortality from age ratios. *Journal of Wildlife Management* 60:37–44.
- White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* 33:942–955.
- 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.
- Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* 81:628–641.
- Wittmer, H. U., B. N. McLellan, D. R. Seip, J. A. Young, T.A. Kinley, G. S. Watts, and D. Hamilton. 2005. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. *Canadian Journal of Zoology* 83: 407–418.

*Associate Editor: Forsyth.*