

# Population Momentum: Implications for Wildlife Management

DAVID N. KOONS,<sup>1</sup> *Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

ROBERT F. ROCKWELL, *Department of Ornithology, American Museum of Natural History, New York, NY 10024, USA*

JAMES B. GRAND, *USGS Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA*

## Abstract

Maintenance of sustainable wildlife populations is one of the primary purposes of wildlife management. Thus, it is important to monitor and manage population growth over time. Sensitivity analysis of the long-term (i.e., asymptotic) population growth rate to changes in the vital rates is commonly used in management to identify the vital rates that contribute most to population growth. Yet, dynamics associated with the long-term population growth rate only pertain to the special case when there is a stable age (or stage) distribution of individuals in the population. Frequently, this assumption is necessary because age structure is rarely estimated. However, management actions can greatly affect the age distribution of a population. For initially growing and declining populations, we instituted hypothetical management targeted at halting the growth or decline of the population, and measured the effects of a changing age structure on the population dynamics. When we changed vital rates, the age structure became unstable and population momentum caused populations to grow differently than that predicted by the long-term population growth rate. Interestingly, changes in fertility actually reversed the direction of short-term population growth, leading to long-term population sizes that were actually smaller or larger than that when fertility was changed. Population momentum can significantly affect population dynamics and will be an important factor in the use of population models for management. (JOURNAL OF WILDLIFE MANAGEMENT 70(1):19–26; 2006)

## Key words

*demography, elasticity, population growth rate, population momentum, population size, sensitivity, transient dynamics.*

In wildlife management, agency and stakeholder goals are often centered on the population, its size, and the change in size over time. To meet these goals, managers often focus on the population growth rate because it can be manipulated to increase population size in the case of conservation (e.g., Fujiwara and Caswell 2001) or decrease size in the case of control (e.g., Rockwell et al. 1997, Merrill et al. 2003).

Sensitivity analysis of the population growth rate to changes in the underlying vital rates (e.g., fecundity, survival, growth, maturation, recruitment, movement) has become a popular tool in wildlife and conservation studies to prioritize management actions aimed at producing change in population growth rate (e.g., Brault and Caswell 1993, Crowder et al. 1994, Doak et al. 1994, Heppell 1998). Sensitivity analysis can help answer important life history and ecology questions as well (e.g., papers within Heppell et al. 2000b, Dobson and Oli 2001, Oli and Dobson 2003).

Nonetheless, predictions made from analytical sensitivity analyses can be unreliable when vital rates change simultaneously by different amounts, as they do in the real world (Citta and Mills 1999, Mills et al. 1999, 2001). Furthermore, analytical sensitivity analyses inherently assume existence of a stable age distribution, which means that calculations depend on the long-term (i.e., asymptotic) population dynamics (de Kroon et al. 2000, Caswell 2001; Ehrlén et al. 2001, Mills and Lindberg 2002). Methods used to examine contributions of stochastically fluctuating vital rates to population growth rate typically focus on asymptotic dynamics also (e.g., life-table response experiments [Horvitz et al. 1997], and life-stage simulation analysis [Wisdom et al. 2000]). Simulation-based sensitivity analyses do not need to assume a

stable age distribution but often do because age distributions are rarely known. When changing a vital rate in a sensitivity analysis, we assume that the change would not perturb the population out of a stable age distribution (Mills and Lindberg 2002). It is unknown how robust this assumption is in wildlife populations (Citta and Mills 1999, Mills and Lindberg 2002).

Management actions can affect vital rates enough to disrupt the age structure. Before the age distribution begins its approach to the stable age distribution after a perturbation, the population size can change rapidly (Neubert et al. 2002). These dynamical responses to an unstable age structure are known as transient dynamics (see Fig. 1), which occur in nature. The cessation of red deer (*Cervus elaphus*) culling on the Isle of Rum, Scotland, has changed the red deer age structure, causing transient population dynamics to persist since culling stopped (Clutton-Brock and Coulson 2002, Coulson et al. 2004). In addition, when examining the potential benefit of turtle-excluder devices on shrimp trawls to loggerhead sea turtle (*Caretta caretta*) populations, Crowder et al. (1994) found that sudden improvements in survival rates caused instability in the age structure. The ensuing transient dynamics resulted in a population size very different than that predicted by asymptotic projections, which essentially is the phenomenon better known as population momentum (Keyfitz 1971; see Fig. 1). Population momentum could occur in wildlife populations when management or large environmental perturbations (e.g., hurricanes, floods, fires, epidemics) cause any vital rate to change by an amount large enough to alter the age structure, but it has not been explicitly examined.

If wildlife populations experience population momentum, estimating the effects of this momentum on population size should be considered when developing conservation and manage-

<sup>1</sup> E-mail: [koons@demogr.mpg.de](mailto:koons@demogr.mpg.de)

ment plans. Here, we use computer simulation to examine the control and conservation of hypothetical wildlife populations. To simulate management practices focused on population growth rate, we halted population growth or decline by changing survival or fertility rates, which often have different elasticity values (Heppell et al. 2000a, Sæther and Bakke 2000). It is often suggested that management focus efforts on the vital rate with the highest elasticity to get the best return in population growth for their effort (Caswell 2000). Yet, we show that short-term population growth and eventual size following some virtual management experiments are so different from the expectations of asymptotic analysis that our findings could influence the way we manage populations for control and conservation.

## Methods

### Data Simulation

To examine population momentum following management actions, we created 3 life histories with stationary asymptotic growth rates ( $\lambda_1 = 1$ ) that mature at 1, 2, and 3 year(s) of age. We designed life histories in which survival rates to age  $i$  ( $P_i$ ) increase with the age of maturity ( $\alpha$ ) and fecundity ( $m$ , the average number of daughters born to a reproductively mature female) decreases, which is the pattern observed across birds and mammals (Sæther 1988, Gaillard et al. 1989, Promislow and Harvey 1990).

In our population model, we calculated fertility ( $F$ ) assuming a prebreeding census ( $F = P_1 * m$ ), with birth occurring at one time of the year. Fertility and the age-specific survival rates for each life history were parameterized into a population projection matrix ( $\mathbf{A}$ ).

$$\mathbf{A} = \begin{bmatrix} F & F & F \\ P_2 & 0 & 0 \\ 0 & P_{3+} & P_{3+} \end{bmatrix} \quad (1)$$

This model assumes conditions under geographic closure and density independence. Although density dependence is ultimately a necessity for all populations, our focus is on rapidly growing or declining populations (see below) in which density feedback on survival or fertility is often negligible.

$$\mathbf{A}_{\alpha_1} = \begin{pmatrix} 0.555 & 0.555 & 0.555 \\ 0.4 & 0 & 0 \\ 0 & 0.5 & 0.5 \end{pmatrix};$$

$$\mathbf{A}_{\alpha_2} = \begin{pmatrix} 0 & 0.286 & 0.286 \\ 0.7 & 0 & 0 \\ 0 & 0.8 & 0.8 \end{pmatrix}; \mathbf{A}_{\alpha_3} = \begin{pmatrix} 0 & 0 & 0.139 \\ 0.8 & 0 & 0 \\ 0 & 0.9 & 0.9 \end{pmatrix}$$

To set up virtual management experiments, we used projection matrices with stationary growth: (fertility values in the top row of each matrix are rounded to the third decimal place), and created growing ( $\lambda_1 = 1.2$ ) populations by multiplying the matrix parameters by 1.2. For the  $\alpha = 3$  life history, multiplication of matrix parameters by 1.2 yielded survival rates  $>1$ ; thus, fertility had to be increased by a greater amount than survival to achieve the desired population growth rate. Hence, we multiplied survival rates by a constant  $C$ , and fertility by  $C^x$ , then solved for  $C$  (solution = 1.104) and  $x$  (solution = 9) simultaneously. Similarly, for each life history, we created declining ( $\lambda_1 = 0.8$ ) populations by multiplying the matrix parameters by 0.8. For only the  $\alpha = 3$  life history, we also created populations initially growing ( $\lambda_1 = 1.35$

and 1.05) or declining ( $\lambda_1 = 0.65$  and 0.95) by greater and lesser amounts in supplemental experiments using a similar application of constants.

### Virtual Management Experiments

Here, we consider populations growing so fast that they could cause environmental damage and populations declining so fast that they could face extinction (i.e., the growing and declining populations defined above). For the  $\alpha = 3$  life history, we also consider populations growing and declining at rates within the common bounds of long-term environmental variation (i.e.,  $\lambda_1 = 1.05$  and 0.95).

Depending on the bird or mammal life history, either survival or fertility may functionally contribute the most to the asymptotic population growth rate and the other the least (Heppell et al. 2000a, Sæther and Bakke 2000). Thus, we focused our experiments on changing adult survival or fertility. In the first set of experiments for each life history, we started with the growing population as the initial condition and then decremented survival rate of adult age classes by the necessary amount to attain stationary asymptotic growth (i.e., the amount required to change  $\lambda_1$  from 1.2 to 1). We performed a similar experiment by decrementing fertility. In the second set of experiments for each life history, we started with the declining population as the initial condition and then augmented survival rate of adult age classes by the necessary amount to achieve stationary asymptotic growth, and then performed similar experiments by augmenting fertility.

To elucidate the effects of managing the asymptotic population growth rate, we assumed that populations initially had a stable age distribution and projected the actual dynamics caused by an unstable age structure following perturbations to a vital rate. We then measured the resulting population momentum ( $M$ ) according to Keyfitz (1971):

$$M = \lim_{t \rightarrow \infty} \frac{\|\mathbf{n}_t\|}{\|\mathbf{n}_0\|} \quad (2)$$

where  $\|\mathbf{n}\|$  is the total population size. This is simply the ratio of the ultimate population size following a perturbation to that immediately before it. To attain exact analytical estimates of population momentum, equation 2 was adjusted to birth-pulse vector form:

$$M = \frac{\mathbf{e}^T (\mathbf{v}_1^{(new)} * \mathbf{w}_1^{(initial)}) \mathbf{w}_1^{(new)}}{\mathbf{e}^T * \mathbf{w}_1^{(initial)}} \quad (3)$$

where  $\mathbf{e}$  is a vector of ones,  $\mathbf{v}_1$  is the dominant left eigenvector of the projection matrix  $\mathbf{A}$  (i.e., the nonscaled age-specific reproductive values),  $\mathbf{w}_1$  is the dominant right eigenvector of the projection matrix (i.e., the nonscaled stable age distribution), "initial" refers to the projection matrix for the initial conditions (growing or declining population), and "new" refers to the projection matrix following changes in adult survival rates or fertility (Caswell 2001:104). Population momentum is measured on a percentage scale centered on 1, thus a momentum of 1.25 means that the population will grow by 25% before eventually reaching the new stable age distribution. Further, a momentum of 1 has zero magnitude. To evaluate the relative importance of momentum, we compared momentum across the management

experiments and across the 3 life histories. Because it was necessary to change vital rates by different amounts to attain the fixed management goal ( $\lambda_1 = 1$ ) in our experiments, we also examined the influence of the proportional change in a vital rate on population momentum.

To compare results from our experiments to predictions from an asymptotic elasticity analysis, we first calculated elasticities (Elasticity =  $\partial \log \lambda_1 / \partial \log \text{vital rate}$ ; de Kroon et al. 1986) for the initially growing and declining populations. Elasticities may provide a better means for comparing the functional contributions of different vital rates to  $\lambda_1$  than sensitivities (Sensitivity =  $\partial \lambda_1 / \partial \text{vital rate}$ ; Caswell 1978) because elasticities are measured on a relative scale (de Kroon et al. 1986, Benton and Grant 1999, but see Link and Doherty 2002). Then we used elasticities to predict the effect of each management experiment on the asymptotic population growth rate for the time step immediately following the vital rate perturbation ( $t \rightarrow t + 1$ ; Heppell 1998, Caswell 2001).

$$\frac{\text{Predicted proportional change in } \lambda_1 \approx \text{Proportional change in vital rate} \times \text{Elasticity}}{\quad} \quad (4)$$

Next, we measured the observed proportional change in the actual population growth rate ( $N_{t+1}/N_t$ ) for the same time step in a way similar to Mills et al. (1999); however, they measured the observed proportional change in  $\lambda_1$  rather than the observed proportional change in  $N_{t+1}/N_t$ .

$$\frac{\text{Observed proportional change in actual growth rate}}{\quad} = \frac{\left( \frac{N_{t+1}/N_t - N_t/N_{t-1}}{N_t/N_{t-1}} \right)}{\quad} \quad (5)$$

Next, we measured the bias of the elasticity prediction, which assumes a stable age distribution following a vital rate perturbation.

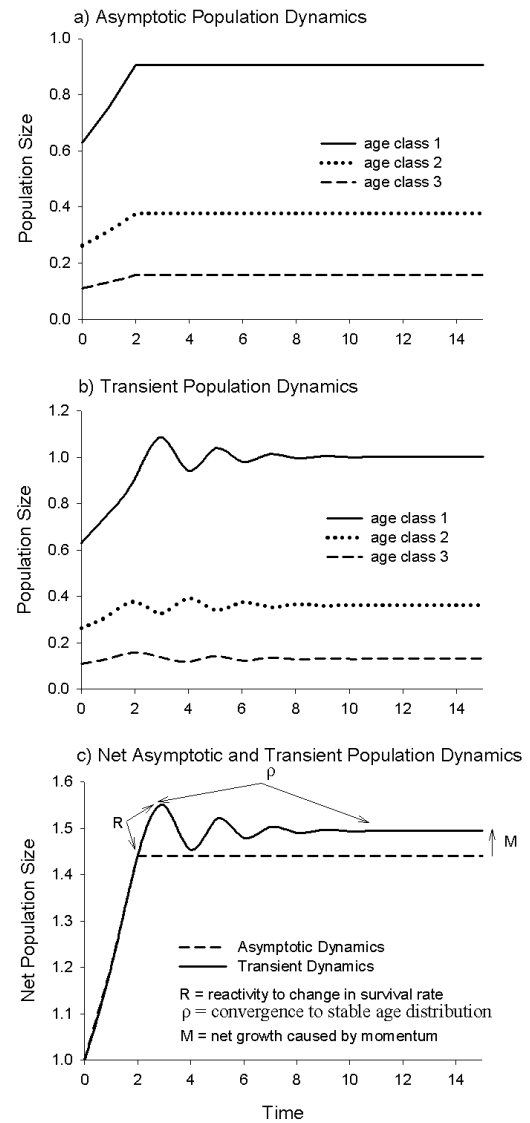
*Bias of elasticity*

$$\text{prediction} = \frac{\text{Predicted proportional change in } \lambda_1 - \text{Observed proportional change in actual growth rate}}{\quad} \quad (6)$$

Finally, we examined the influence of the proportional change in a vital rate on the bias of the elasticity prediction.

## Results

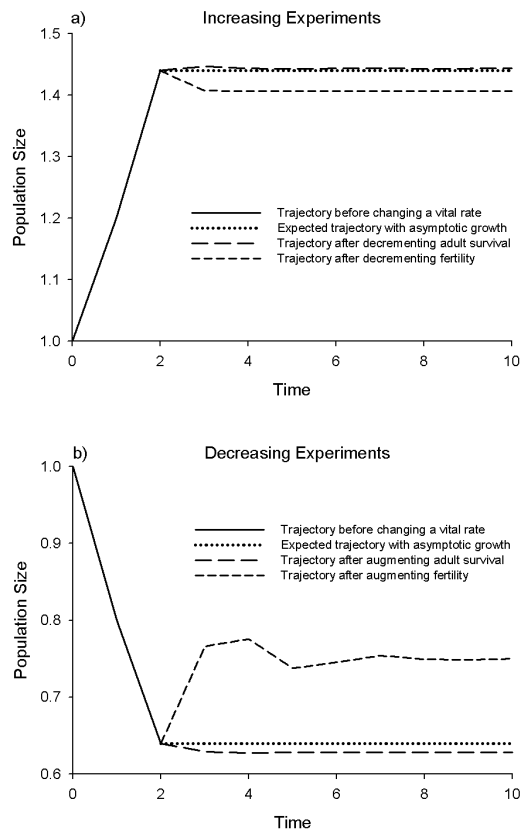
Using Keyfitz's measurement of population momentum, we estimated the actual effect of instantaneous vital rate changes on age structure, short-term population growth, and long-term population size. The initially increasing populations of the  $\alpha = 1, 2,$  and  $3$  life histories had 52, 17, and 10% more adults in the last age class, respectively, relative to the stable age distribution following the decrement in adult survival. The initially decreasing populations had 30, 12, and 5% fewer adults in the last age class relative to the stable age distribution following augmentation of adult survival. As a result, the direction of population momentum for each life history was consistent with the historical pattern of growth (Fig. 2), and was small in magnitude (absolute magnitude  $\leq 0.045$ ). Moreover, the actual population growth rate rapidly stabilized to the asymptotic stationary rate (e.g., see Fig. 2) for life histories that had high adult survival elasticities (Table 1). We also



**Figure 1.** An example of a population with 3 age classes growing at the rate of  $\lambda_1 = 1.2$  until the second time step, when survival rate is changed to produce stationary asymptotic growth ( $\lambda_1 = 1$ ). In (a), we show continual asymptotic growth following the changed survival rate, which can only happen if the population somehow transitions automatically to the new stable age distribution. In (b), we show the oscillating transient dynamics that would actually occur (barring direct manipulation of the age distribution by managers) after the survival rate is changed. In (c), the age classes are summed together to depict the projected net population size for each scenario (a and b), and we show how the population initially reacts (reactivity  $R$ ) to the changed survival rate, how long it takes the population to reach a stable age distribution (convergence  $\rho$ ), and the net increase in size caused by population momentum (momentum  $M$ ).

detected a small negative relationship between age at maturity and the magnitude of population momentum for the increasing population experiment, and we detected a small positive relationship for the decreasing population experiment (Fig. 3).

The effects of changing fertility contrasted with the findings for changes in adult survival (Figs. 2, 3). Surprisingly, the initially increasing populations of the  $\alpha = 1, 2,$  and  $3$  life histories all had 32% fewer adults in the last age class relative to the stable age distribution following the decrement in fertility. The initially decreasing populations all had 60% more adults in the last age



**Figure 2.** Population projections of the  $\alpha = 3$  life history for the standard increasing (a;  $\lambda_1 = 1.2$ ) and decreasing (b;  $\lambda_1 = 0.8$ ) population experiments. Across experiments, either adult survival rate or fertility was changed at the second time step to achieve stationary asymptotic growth ( $\lambda_1 = 1.0$ ). Results were similar for the other life histories except the transient dynamics and resulting population momentum values were generally of lesser magnitude.

class relative to the stable age distribution following augmentation of fertility. As a result, the initially growing populations decreased and the initially declining populations increased (Fig. 2). Thus, changes in fertility—which had the lowest asymptotic elasticity for the  $\alpha = 2$  and 3 life histories (Table 1)—caused population size to change in a more desirable direction for control and conservation purposes. Furthermore, in experiments with decreasing populations, the magnitude of momentum resulting from changes in

fertility increased with age at maturity of the life histories (Fig. 3). Populations reacted more to changes in fertility than to changes in adult survival rates (e.g., see change in population size from time step 2 to 3 in Fig. 2). As a result, magnitudes of momentum in the experiments were much larger (as much as 0.17) than those produced by changes in adult survival (Fig. 3), except in the increasing population experiment for the  $\alpha = 1$  life history. Because fertility often had a small elasticity value, it had to be changed by large amounts to achieve stationary population growth. Large changes in a vital rate cause large perturbations to the age structure (see above), which then causes the magnitude of population momentum to increase. This explains why the magnitude of momentum was larger following changes in fertility versus changes in adult survival (Fig. 4).

When we considered the supplemental population experiments for the  $\alpha = 3$  life history, the magnitude of population momentum increased as the difference between the initial population growth rate and the management objective ( $\lambda_1 = 1.00$ ) increased. This relationship was most pronounced when fertility was decremented in the decreasing population experiments (Fig. 5). Once again, these results were influenced by the proportional change in a vital rate that was required to achieve the management objective ( $\lambda_1 = 1.00$ ; Fig. 4).

Additionally, we detected substantial bias when using elasticity values to predict the proportional change in population growth rate following a given proportional change in a vital rate. As the proportional change in adult survival rate increased, the absolute value of the bias in the elasticity prediction also increased. Furthermore, the bias was high for increases in adult survival and low for decreases in adult survival (Fig. 6). Thus, the direction of bias was consistent with the direction of change in adult survival. When the proportional change in fertility increased, the absolute value of the bias in the elasticity prediction also increased, similar to the results for changes in adult survival. However, the bias was low for decreases in fertility and high for increases in fertility (Fig. 6), which occurred because the unstable age structure caused the direction of population growth to change following perturbations to fertility.

## Discussion

Maintenance of sustainable wildlife populations is one of the primary purposes of wildlife management. Thus, understanding

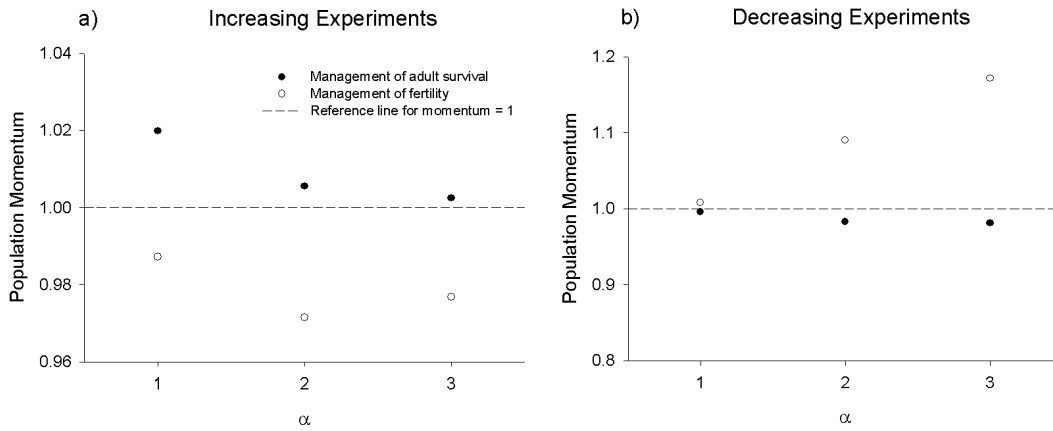
**Table 1.** Vital rate elasticity values for populations initially growing ( $\lambda_1 = 1.2$ ) and declining ( $\lambda_1 = 0.8$ ) across the 3 life histories ( $\alpha = 1, 2, 3$ ).

| Elasticity values <sup>a</sup> |                     |                   |                |                       |                   |                |
|--------------------------------|---------------------|-------------------|----------------|-----------------------|-------------------|----------------|
| $\alpha$                       | Growing populations |                   |                | Declining populations |                   |                |
|                                | Fertility           | Subadult survival | Adult survival | Fertility             | Subadult survival | Adult survival |
| 1                              | 0.53                |                   | 0.47           | 0.53                  |                   | 0.47           |
| 2                              | 0.16                | 0.17              | 0.67           | 0.16                  | 0.17              | 0.67           |
| 3                              | 0.13                | 0.25              | 0.62           | 0.08                  | 0.17              | 0.75           |
| 3 <sup>b</sup>                 | 0.17                | 0.34              | 0.49           | 0.08                  | 0.17              | 0.75           |
| 3 <sup>c</sup>                 | 0.08                | 0.17              | 0.75           | 0.08                  | 0.17              | 0.75           |

<sup>a</sup> Elasticities are summed across the relevant age classes and rounded to 2 decimal places.

<sup>b</sup> Additional results for populations of the  $\alpha = 3$  life history initially growing ( $\lambda_1 = 1.35$ ) or declining ( $\lambda_1 = 0.65$ ) at a greater rate than in the standard experiments. Whenever a matrix is multiplied by a constant (C), the eigenvalues are simply scaled by the constant and the eigenvector structure does not change. Thus, elasticity values do not change.

<sup>c</sup> Additional results for populations of the  $\alpha = 3$  life history initially growing ( $\lambda_1 = 1.05$ ) or declining ( $\lambda_1 = 0.95$ ) at a lesser rate than in the standard experiments.



**Figure 3.** Population momentum values across all life histories ( $\alpha = 1, 2, 3$ ) for the standard increasing (a;  $\lambda_1 = 1.2$ ) and decreasing (b;  $\lambda_1 = 0.8$ ) population experiments where adult survival or fertility was manipulated. The scaling of the y-axis differs between (a) and (b).

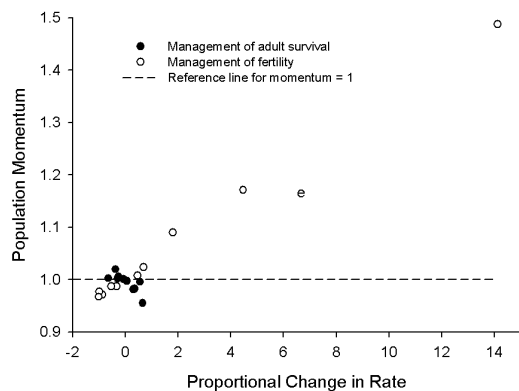
the true nature of management actions on population dynamics should be of fundamental importance to wildlife biologists. Asymptotic sensitivity analysis has become a popular tool in wildlife biology because it can elucidate efficient means of managing vital rates for optimal returns in population growth rate and size (e.g., Doak et al. 1994, Rockwell et al. 1997, Wisdom and Mills 1997, Hoekman et al. 2002). However, empirical evidence indicates that asymptotic measures do not always capture the actual dynamics that occur in nature (Bierzychudek 1999, Clutton-Brock and Coulson 2002, Coulson et al. 2004, Franklin et al. 2004).

In fact, management actions themselves can affect a population's age structure (Crowder et al. 1994, Coulson et al. 2004). In our population experiments, changes in vital rates did perturb populations out of the stable age distribution. As a result, we found that asymptotic elasticity values did not accurately predict the proportional change in population growth rate following a given proportional change in a vital rate (Fig. 6). Thus, we conclude that predictions made from asymptotic elasticities are not robust to the inherent assumption of a stable age distribution. Analytical solutions for examining the sensitivity of the transient population growth rate (Yearsley 2004, D. N. Koons et al., Auburn University, unpublished data) and size (Fox and Gurevitch 2000) now exist for cases when age structure is unstable, but known. Age structure is rarely known, but if it is, we

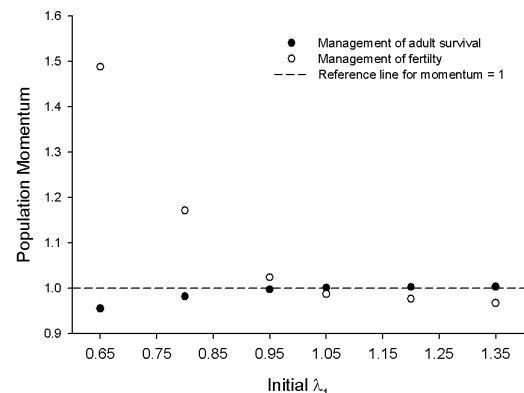
suggest using these methods to examine ecological questions and to guide management practices.

For stable age-structured populations that were growing or declining, we used matrix models to show that management actions that suddenly changed vital rates to achieve stationary growth can result in population momentum. Similarly, management actions that attempt to change the direction of long-term population growth (e.g., changing  $\lambda_1$  from 1.2 to 0.97, or from 0.8 to 1.03) result in population momentum values quite similar to those presented in our paper ( $<0.016$  units of difference; D. N. Koons, Auburn University, unpublished data). Population momentum has a lasting effect on population size in ways not revealed by asymptotic analyses, and we show that momentum varies with life history and depends on the specific vital rate that is changed and the proportional change that is made to a vital rate.

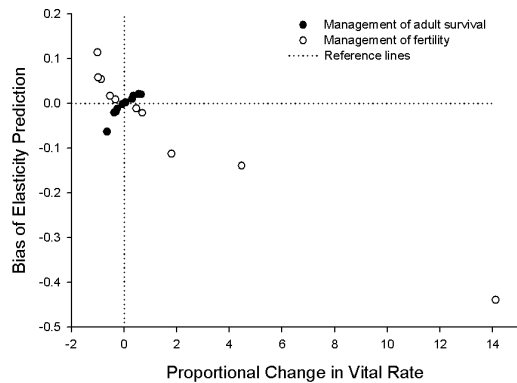
Population momentum is a complicated process that proximately depends on how changes in a vital rate affect the age structure (eq. 3). For example, the number of adults in the initial population relative to the stable age distribution that was eventually attained following the virtual management experiment depended on the vital rate that was changed (i.e., adult survival or fertility). Populations that initially had a surplus of older adults experienced positive population growth and positive ( $>1$ ) population momentum, and populations that initially had deficits of older adults



**Figure 4.** The magnitude of population momentum as it relates to the proportional change made to a vital rate across all the population experiments and life histories.



**Figure 5.** Population momentum values across all population experiments for the  $\alpha = 3$  life history in which adult survival or fertility was manipulated.



**Figure 6.** The relationship between the bias produced by the predicted proportional change in population growth rate (based on elasticity of each vital rate in the initial-condition matrices, Table 1) relative to the observed proportional change in population growth rate (y-axis), and the proportional change made to each vital rate (x-axis) across all the population experiments and life histories. The x-axis is measured on a proportional scale; thus, a value of 4 indicates a fourfold increase. The y-axis measures the difference between 2 proportional measures.

experienced negative population growth and negative (<1) population momentum. Caswell (2001:106) also found that the direction of population momentum depended on the initial surplus or deficit of adults in a stage-structured model. Thus, clearly the initial age (or stage) structure relative to that following changes in a vital rate will dictate the direction of short-term population growth and momentum.

While the direction of population momentum is determined by the specific vital rate that is changed, the magnitude of population momentum is influenced by the magnitude of change in the vital rate. Large changes in a vital rate will produce large changes in the age structure and thus the equilibrium population size.

We also found a relationship between population momentum and life history (Fig. 3), which was driven by a pattern in the transient dynamics caused by the experimental perturbations we implemented. Perturbations to the age distribution of populations with short generation lengths are assuaged quickly because of rapid population turnover, and the converse is true for animals with long generation lengths (Tuljapurkar 1985). Still, oscillations in the age structure (see Fig. 1) may take a long time to converge to the stable age distribution but cause little change in the net population size. Recently, D. N. Koons et al. (Auburn University, unpublished data) have found that transient population growth rates among late-maturing, long-lived birds and mammals are initially reactive to direct changes in age structure, but less so for early-maturing, short-lived species. This initial reaction to a perturbation can have a lasting effect on the long-term population size (Figs. 1, 2; Neubert et al. 2002). Thus, we believe that the reactivity of a population to perturbations is the primary factor driving patterns of population momentum across life histories, and that the time required for a population to return to a stable age distribution plays a secondary role. Nevertheless, more work will be required to quantitatively establish the connection between life history and population momentum.

Our studies considered population momentum following 1-time perturbations to life histories with exponential growth in otherwise constant environments. In addition, our goal was to examine

population dynamics following vital rate perturbations in a fashion that is one step closer to reality than that assumed under asymptotic sensitivity analysis. The virtual management experiments were not meant to represent reality. Fertility in our models was the product of fecundity and survival to the first birthday. Thus, it would be interesting to examine the response of population momentum to changes in these lower-level life-history parameters as well as the seasonal components of survival (e.g., survival of young to fledging, winter survival, etc.). In some populations, density dependence may cause vital rates to change more slowly over time than the instantaneous changes considered here. Li and Tuljapurkar (1999) found that momentum increases with the time it takes to attain the vital rate goal. Thus, momentum could have strong effects on populations regulated by density dependence, and future management studies should build on our findings by examining population momentum in these environments and others (e.g., stochastic and periodic environments).

## Research and Management Implications

Population momentum could push populations far past an environmental carrying capacity or even to extinction, depending on the direction of momentum. By affecting the long-term population trajectory, momentum could shorten or lengthen the time it takes for a population to become extinct or recover from a perturbation, relative to that projected with an asymptotic analysis (e.g., Merrill et al. 2003). Thus, population momentum should be considered in population viability analyses (sensu Gilpin and Soulé 1986).

These matters and others should be of concern to wildlife managers when management goals are centered on both population size and growth rate (e.g., North American Waterfowl Management Plan). If population size is already too large or too small, managing the asymptotic population growth rate may be inefficient. For example, we might prefer a management action that can initially reduce or increase the population size, and at the same time produce the desired population growth rate in the future. It is conceivable that managers could actually use population momentum to their advantage to achieve such a goal. For example, even if fertility has a low elasticity value, it may be more feasible to change fertility than adult survival. Our results indicate that changing fertility produces short-term population growth and momentum that is consistently in a desirable direction for population control or conservation, but changing adult survival does not. In our prebreeding census models, fertility was the product of fecundity and survival to the first birthday. Depending on the organism, managers may find it easier to manipulate fecundity (e.g., releasing hatchery-reared young) or survival to the first birthday (e.g., improving fawn survival or chick survival).

Animal harvest can also affect vital rates such as survival (e.g., additive harvest), and it can alter the structure of a population (e.g., slot limits in fisheries, trophy management of ungulates). Thus, it seems highly probable that harvest management could cause population momentum, and in turn affect population size and the sustainability of harvest itself. Yet, population dynamics operating under the pressures of harvest are thought to follow density-dependent processes. Our results only pertain to density-independent population growth. Thus, more work will be required

to elucidate the possible effects of harvest on population momentum in density-dependent systems.

To more accurately examine the actual effects of vital rate management on population dynamics, it will be necessary for field biologists to collect data on population age distributions (e.g., Coulson et al. 2004). Knowledge of age distributions could alleviate the reliance of management actions based on asymptotic population analysis. If age distributions can be estimated, we can determine whether wild populations are close to their stable age distributions. If so, then asymptotic sensitivity analysis might be useful to wildlife managers; however, if not, the tools presented here and by others (Fox and Gurevitch 2000, Yearsley 2004, D. N. Koons et al., Auburn University, unpublished data) will be more useful. Last, incorporation of age distribution estimates into population models will allow us to more accurately examine past and future population dynamics. For example, it is believed that fluctuations in population growth rate and size in wild populations are caused by stochastic fluctuations in the vital rates. However,

observed fluctuations in population growth rate and size are partially caused deterministically by unstable age structures (e.g., the transient dynamics and population momentum). Understanding the actual influence of age structure on population dynamics in the wild will improve our knowledge about population dynamics as a whole (Clutton-Brock and Coulson 2002, Coulson et al. 2004).

## Acknowledgments

We thank L. S. Mills, S. Heppell, J. Rotella, P. Flint, F. S. Dobson, and J. Arnold for their comments on our manuscript. We particularly appreciate the support of D. V. Derksen and L. K. Thorsteinson of USGS, Biological Resources Division. The USGS, Biological Resources Division, Alaska Biological Science Center funded this research. This research addresses a priority identified by the Minerals Management Service, Alaska Outer Continental Shelf Region.

## Literature Cited

- Benton, T. G., and A. Grant. 1999. Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* 14: 467–471.
- Bierzychudek, P. 1999. Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications* 9:1278–1287.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (*Orcinus orca*). *Ecology* 74:1444–1454.
- Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology* 14:215–230.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* 81:619–627.
- Caswell, H. 2001. Matrix population models. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Citta, J. J., and L. S. Mills. 1999. What do demographic sensitivity analyses tell us about controlling brown-headed cowbirds? *Studies in Avian Biology* 18: 121–134.
- Clutton-Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London, B* 357:1285–1298.
- Coulson, T., F. Guinness, J. Pemberton, and T.H. Clutton-Brock. 2004. The demographic consequences of releasing a population of red deer from culling. *Ecology* 85:411–422.
- Crowder, L. B., D. T. Crouse, S. S. Heppell, and T. H. Martin. 1994. Predicting the impact of turtle-excluder devices on loggerhead sea turtle populations. *Ecological Applications* 4:437–445.
- de Kroon, H., A. Plaiser, J. van Groenendaal, and H. Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67:1427–1431.
- de Kroon, H., J. van Groenendaal, and J. Ehrlén. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81:607–618.
- Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. *Ecological Applications* 4: 446–460.
- Dobson, F. S., and M. K. Oli. 2001. The demographic basis of population regulation in Columbian ground squirrels. *American Naturalist* 158:236–247.
- Ehrlén, J., J. van Groenendaal, and H. de Kroon. 2001. Reliability of elasticity analysis: reply to Mills et al. *Conservation Biology* 15:278–280.
- Fox, G. A., and J. Gurevitch. 2000. Population numbers count: tools for near-term demographic analysis. *American Naturalist* 156:242–256.
- Franklin, A. B., R. J. Gutiérrez, J. D. Nichols, M. E. Seamans, G. C. White, G. S. Zimmerman, J. E. Hines, T. E. Munton, W. S. LaHaye, J. A. Blakesley, G. N. Steger, B. R. Noon, D. W. H. Shaw, J. J. Keane, T. L. McDonald, and S. Britting. 2004. Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs* 54:1–54.
- Fujiwara, M., and H. Caswell. 2001. Demography of the endangered North Atlantic right whale. *Nature* 414:537–541.
- Gaillard, J. -M., D. Pontier, D. Allainé, J. D. Lebreton, and J. Trouvilliez. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* 56:59–76.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: processes of species extinction. 19–34 M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375.
- Heppell, S. S., H. Caswell, and L. B. Crowder. 2000a. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81:654–665.
- Heppell, S. S., C. Pfister, and H. de Kroon. 2000b. Elasticity analysis in population biology: methods and applications. *Ecology* 81:606–606.
- Hoekman, S. T., L. S. Mills, D. W. Howter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analysis of the life history of midcontinent mallards. *Journal of Wildlife Management* 66:883–900.
- Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The “importance” of life history stages to population growth: prospective and retrospective analyses. 247–272 S. Tuljapurkar, and H. Caswell, editors. *Structured population models in marine, terrestrial and freshwater systems*. Chapman and Hall, New York, New York, USA.
- Keyfitz, N. 1971. On the momentum of population growth. *Demography* 8:71–80.
- Li, N., and S. Tuljapurkar. 1999. Population momentum for gradual demographic transitions. *Population Studies* 53:255–262.
- Link, W. A., and P. F. Doherty, Jr. 2002. Scaling in sensitivity analysis. *Ecology* 83:3299–3305.
- Merrill, J. A., E. G. Cooch, and P. D. Curtis. 2003. Time to reduction: factors influencing management efficacy in sterilizing overabundant white-tailed deer. *Journal of Wildlife Management* 67:267–279.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conservation Biology* 13:815–829.
- Mills, L. S., D. F. Doak, and M. J. Wisdom. 2001. Elasticity analysis for conservation decision making: reply to Ehrlén et al. *Conservation Biology* 15: 281–283.
- Mills, L. S., and M. S. Lindberg. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. 338–366 S. R. Beissinger, and D. R. McCullough, editors. *Population viability analysis*. The University of Chicago, Chicago, Illinois, USA.
- Neubert, M. G., H. Caswell, and J. D. Murray. 2002. Transient dynamics and pattern formation: reactivity is necessary for Turing instabilities. *Mathematical Biosciences* 175:1–11.
- Oli, M. K., and F. S. Dobson. 2003. The relative importance of life-history

- variables to population growth rate in mammals: Cole's prediction revisited. *American Naturalist* 161:422–440.
- Promislow, D. E. L., and P. H. Harvey. 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. *Journal of Zoology* 220:417–437.
- Rockwell, R. F., E. G. Cooch, and S. Brault. 1997. High goose populations: causes, impacts and implications. 73–100 B. J. Batt, editor. *Arctic ecosystems in peril: report of the arctic goose habitat working group*. Arctic goose joint venture special publication. U.S. Fish and Wildlife Service, Washington DC, USA.
- Sæther, B.-E. 1988. Pattern of covariation between life history traits of European birds. *Nature* 331:616–627.
- Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- Tuljapurkar, S. D. 1985. Population dynamics in variable environments. VI. Cyclical environments. *Theoretical Population Biology* 28:1–17.
- 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.
- Yearsley, J. M. 2004. Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling* 177:245–258.

*Associate Editor: Mills.*