Ecology, 88(11), 2007, pp. 2857–2867

POPULATION INERTIA AND ITS SENSITIVITY TO CHANGES IN VITAL RATES AND POPULATION STRUCTURE

David N. Koons,[1,2,5] Randall R. Holmes,[3] and James B. Grand[4]

[1]*Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences,*
Auburn University, Alabama 36849-5418 USA
[2]*Max Planck Institute for Demographic Research, Konrad-Zuse Strasse 1, D-18057 Rostock, Germany*
[3]*Department of Mathematics and Statistics, College of Science and Mathematics, Auburn University, Alabama 36849-5310 USA*
[4]*USGS Alabama Cooperative Fish and Wildlife Research Unit, School of Forestry and Wildlife Sciences,*
Auburn University, Alabama 36849-5418 USA

Abstract. Because the (st)age structure of a population may rarely be stable, studies of transient population dynamics and population momentum are becoming ever more popular. Yet, studies of "population momentum" are restricted in the sense that they describe the inertia of population size resulting from a demographic transition to the stationary population growth rate. Although rarely mentioned, inertia in population size is a general phenomenon and can be produced by any demographic transition or perturbation. Because population size is of central importance in demography, conservation, and management, formulas relating the sensitivity of population inertia to changes in underlying vital rates and population structure could provide much-needed insight into the dynamics of populations with unstable (st)age structure. Here, we derive such formulas, which are readily computable, and provide examples of their potential use in studies of life history and applied arenas of population study.

Key words: inertia; life history; population momentum; population structure; sensitivity; stable age distribution; stable equivalent ratio.

Introduction

Population size is central to the fields of demography and population biology. Demographers often study population size because it can affect economies, policy, social dynamics, and even natural resource supplies (Bos et al. 1994, Fischer and Heilig 1997, United Nations 2003). Biologists pay special attention to population size when trying to understand ecological processes, keep small populations from going extinct, controlling pest populations, and in management of populations that provide hunting, fishing, and viewing opportunities as well as world-market food resources (Caughley 1977). Additionally, the change in population size over time (i.e., population growth rate) describes the average fitness and performance of the population (Fisher 1930, Sibly et al. 2002). Thus, population size is an important parameter for many reasons.

In population modeling, it is common to assume a stable population structure (i.e., the distribution of abundance across age, stage, body size, sex, spatial location, or other categories) and examine how underlying vital rates, such as fecundity and survival, affect long-term population size and rate of growth (e.g., λ). Unfortunately, this assumption is rarely met in nature (Fox and Gurevitch 2000). Population structure is usually unstable (e.g., an underabundance of prime-aged adults) resulting in transient dynamics (i.e., unstable short-term dynamics [Coale 1972, Clutton-Brock and Coulson 2002]). Depending on the relative overabundance vs. underabundance of particular phenotypic classes (e.g., adults vs. offspring), the initial transient reaction to an unstable population structure can lead to sudden and substantial increases or decreases in population size (Caswell and Neubert 2005; Fig. 1a). In addition to the particular instability of population structure (Merrill et al. 2003), an organism's generation time will influence the rate at which stable population structure is achieved and the magnitude of transient fluctuations in abundance en route to the stable dynamics (Koons et al. 2005). These unstable short-term dynamics can in turn produce an inertial effect on long-term population size causing it to be larger or smaller than that of an otherwise equivalent population that always has a stable population structure (Tuljapurkar and Lee 1997), which we call "population inertia" (see Fig. 1a).

The most commonly studied case of population inertia is Keyfitz's concept of population momentum (1971*a*), which pertains to the special case when a population's vital rates undergo a change to the stationary level (i.e., the level of lifetime individual replacement; see Fig. 1b). Population momentum has been studied extensively in human demography and its effect has been shown to occur in many populations

---

Manuscript received 30 October 2006; revised 22 February 2007; accepted 5 March 2007. Corresponding Editor: E. G. Cooch.

[5] Present address: Department of Wildland Resources and the Ecology Center, Utah State University, 5230 Old Main Hill, Logan, Utah 84322 USA.
E-mail: david.koons@usu.edu

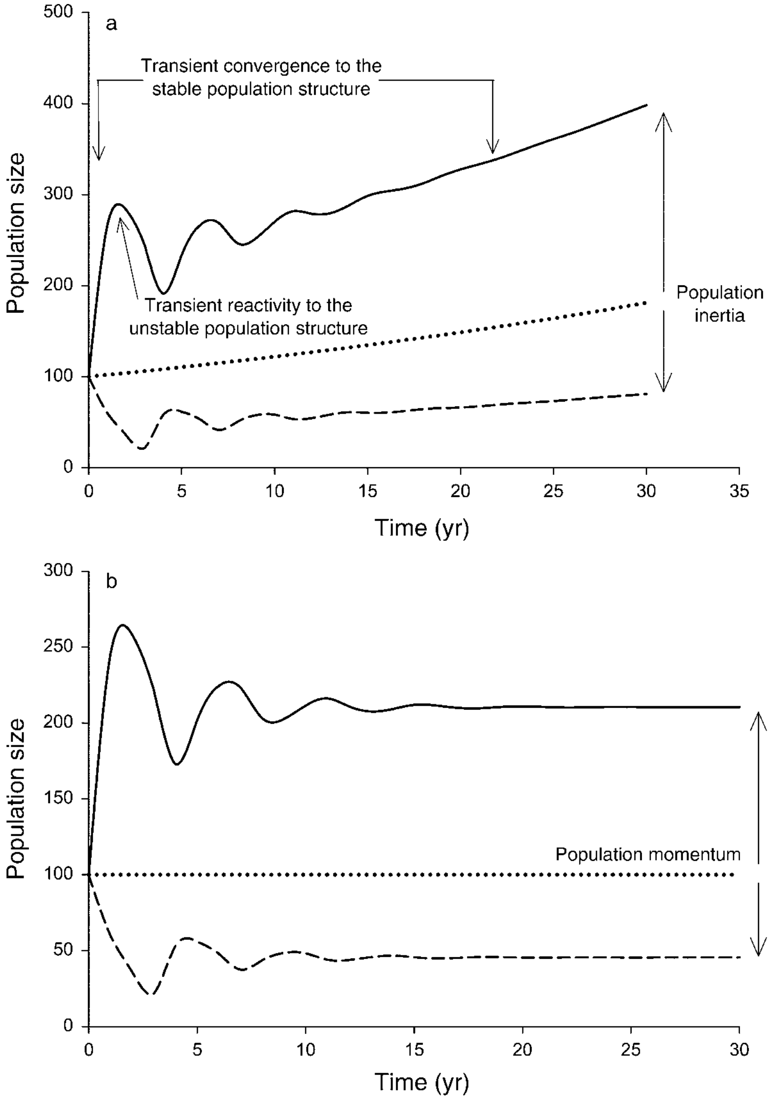

FIG. 1. (a) When a population's structure becomes unstable, there is an initial transient reaction that can cause a sudden increase or decrease in population size followed by transient fluctuations in size that decrease in magnitude as structure converges to the stable population structure. Depending on the relative overabundance vs. underabundance of particular phenotypic classes (e.g., adults vs. offspring), the eventual result of unstable population structure can be an inertial augmentation (solid lines) or reduction (dashed lines) of population size relative to the size of an otherwise equivalent population growing (or declining, which is not shown here) according to its stable population structure (dotted lines). Measures of population inertia are given in *Derivation of population inertia sensitivities*. (b) Graphical examples of Keyfitz's "population momentum," which is just a special case of population inertia for populations whose long-term rate of growth is stationary.

(e.g., Keyfitz 1971*a*, Frauenthal 1975, Mitra 1976, Wachter 1988, Schoen and Kim 1991, 1998, Fischer and Heilig 1997, Kim and Schoen 1997, Bongaarts and Bulatao 1999, Li and Tuljapurkar 1999, 2000, Goldstein 2002, Schoen and Jonsson 2003). Biologists have recently shown that population momentum (Hauser et al. 2006, Koons et al. 2006*a*, *b*) and each of the aforementioned aspects of transient dynamics will be of critical importance in conservation and management of wild populations because of the insight they provide into dynamics of realistic populations with unstable structure (Fox and Gurevitch 2000, Merrill et al. 2003, Yearsley 2004, Koons et al. 2005, Mertens et al. 2006, Caswell 2007). Population inertia is more general than Keyfitz's momentum and applies to growing, declining, spatially structured, and density-regulated populations, as well as those inhabiting stochastic environments (assuming weak demographic ergodicity); however, it is rarely considered in scientific studies (but see Tuljapurkar and Lee 1997).

Like population growth rate, population inertia can influence chances of extinction as well as the time required to achieve population goals (Koons et al. 2006*b*). Thus, tools that relate change in underlying demographic parameters to change in population inertia could benefit biologists as well as human demographers. The sensitivity of population growth rate to changes in underlying vital rates has a long history of use in demography and evolutionary theory (Lewontin 1965, Hamilton 1966, Demetrius 1969, Emlen 1970, Goodman 1971, Keyfitz 1971*b*, Mertz 1971), and Caswell's (1978) discrete-time sensitivity formula has made calculation of this metric relatively simple for empiricists to use (e.g., van Groenendael et al. 1988, Horvitz et al. 1997, Benton and Grant 1999; papers within Heppell et al. 2000). Analogous analytical formulae for population inertia have not been developed but could be useful for comparing the effects of alternative policies or management actions on population inertia and goals related to population size. Here, we present such formulae for the sensitivity of population inertia to changes in any vital rate or population structure. Using examples, we show how these formulae can be used to examine the implications of population inertia on the abundance of populations open to migration (including source–sink populations), the implications for conservation and management, and the relevance to comparative live history analysis.

Derivation of Population Inertia Sensitivities

Population model and notation

We use boldface capital letters to denote matrices and boldface lowercase letters to denote vectors. We use $\bar{x}$ to denote the conjugate of x, $\mathbf{x}^\top$ to denote the transpose of the vector $\mathbf{x}$ and $\mathbf{x}^*$ to denote the complex conjugate transpose.

Our derivation is based on a linear, discrete, time-invariant matrix population model:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t. \tag{1}$$

Here, $\mathbf{n}_t$ is an n-dimensional vector with ith entry $n_i(t)$ equal to the number of individuals in the ith stage at time t. $\mathbf{A}$ is an $n \times n$ matrix with (i, j)-entry a_{ij} equal to the transition rate from the jth stage to the ith stage. Alternatively, the population vector at any time t can be expressed as

$$\mathbf{n}_t = \sum_{i=1}^{n} c_i \lambda_i^t \mathbf{w}_i \tag{2}$$

where the λ_i's are the eigenvalues of $\mathbf{A}$ (which we assume to be distinct), the $\mathbf{w}_i$'s are corresponding right eigenvectors, and the c_i's depend on initial conditions and satisfy

$$\mathbf{n}_0 = \sum_{i=1}^{n} c_i \mathbf{w}_i$$

(Caswell 2001). The ith eigenvalue λ_i and corresponding right $\mathbf{w}_i$ and left $\mathbf{v}_i$ eigenvectors of $\mathbf{A}$ satisfy

$$\mathbf{A}\mathbf{w}_i = \lambda_i \mathbf{w}_i \tag{3}$$

$$\mathbf{v}_i^* \mathbf{A} = \lambda_i \mathbf{v}_i^*. \tag{4}$$

Unless otherwise stated, we assume that $\mathbf{A}$ is primitive so that, according to the Perron-Frobenius theorem (Gantmacher 1959, Seneta 1981, Horn and Johnson 1985), there is a unique eigenvalue of $\mathbf{A}$ having modulus strictly larger than the moduli of the other eigenvalues. The indexing is chosen in such a way that λ_1 is this "dominant" eigenvalue. It is real and positive, and both $\mathbf{w}_1$ and $\mathbf{v}_1$ have real positive entries. For large t, the $i = 1$ term dominates the expression for $\mathbf{n}_t$ given in Eq. 2, and so eventually, the population grows approximately geometrically at the rate λ_1 (assuming $c_1 \neq 0$). The dominant right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors describe the asymptotic population structure and reproductive values, respectively (Goodman 1968). Unless otherwise noted, we assume that the eigenvectors have been scaled so that $\mathbf{v}_i^*\mathbf{w}_i = 1$, and $\mathbf{v}_i^*\mathbf{w}_j = 0$ for $i \neq j$. We further assume that $||\mathbf{w}_1|| = 1$ and $\mathbf{v}_1$ is real, where the 1-norm of any vector $\mathbf{x}$ is denoted by $||\mathbf{x}|| = \Sigma_{i=1}^{n} x_i$ (x_i is the ith component of x).

Measurement of population inertia

Population inertia measures the long-term abundance of a population with any historical structure (Fig. 1, dashed or solid lines) relative to the expected abundance of an otherwise equivalent population growing according to its stable population structure (Fig. 1, dotted lines). Population inertia is thus measured with a ratio, and in demography, it has been called the stable equivalent ratio (SER; sensu Tuljapurkar and Lee 1997). It is important to note that large magnitudes of population inertia (i.e., SERs differing greatly from 1) signify populations whose long-term abundance is greatly affected by historical structure, not ones that are resistant to the effects of historical population structure.

In order to relate various notions of population inertia and momentum that have appeared in the literature, we first consider a general definition of inertia

$$I_{\mathbf{r}_0} = \lim_{t\to\infty} \frac{||\mathbf{n}_t||\,||\mathbf{r}_0||}{||\mathbf{r}_t||\,||\mathbf{n}_0||} \tag{5}$$

which we call the "inertia I relative to $\mathbf{r}_0$." Here $\mathbf{r}_0$ is a nonzero vector and $\mathbf{r}_t = \mathbf{A}^t\mathbf{r}_0$. We regard $\mathbf{r}_0$ as a point of reference and therefore call it the "reference vector." In Appendix A, we establish the following: by assuming that $\mathbf{r}_0 = c\mathbf{w}_1$ for some positive real number c, Eq. 5 yields the SER mentioned above:

$$\mathrm{SER} = \frac{\mathbf{v}_1^*\mathbf{n}_0||\mathbf{r}_0||}{\mathbf{v}_1^*\mathbf{r}_0||\mathbf{n}_0||}. \tag{6}$$

If we further assume that $\mathbf{r}_0$ is of the same size as $\mathbf{n}_0$ (i.e., $||\mathbf{r}_0|| = ||\mathbf{n}_0||$), then the SER reduces to

$$\mathrm{SER} = \frac{\mathbf{v}_1^*\mathbf{n}_0}{\mathbf{v}_1^*\mathbf{r}_0} \tag{7}$$

which is consistent with Eq. 7 in Tuljapurkar and Lee (1997). Next, by replacing $\mathbf{r}_0$ in Eq. 6 with $c\mathbf{w}_1$ and canceling c's we attain

$$\mathrm{SER} = \frac{\mathbf{v}_1^* \mathbf{n}_0 ||\mathbf{w}_1||}{\mathbf{v}_1^* \mathbf{w}_1 ||\mathbf{n}_0||} = \frac{\mathbf{e}^\top (\mathbf{v}_1^* \mathbf{n}_0) \mathbf{w}_1}{\mathbf{e}^\top \mathbf{n}_0} \tag{8}$$

where $\mathbf{e}$ is the vector with each entry equal to one. The right-hand side of Eq. 8 is the same as Caswell's discrete-time formula for population momentum (Caswell 2001:104). Caswell considers momentum resulting from instantaneous demographic changes to the stationary level, that is, where $\lambda_1 = 1$. In this case, $\mathbf{r}_t = c\mathbf{w}_1 = \mathbf{r}_0$ for all t so Eq. 5 gives

$$\mathrm{SER}_K = \lim_{t\to\infty} \frac{||\mathbf{n}_t||}{||\mathbf{n}_0||} \qquad (\text{assuming } \lambda_1 = 1) \tag{9}$$

which is equivalent to Keyfitz's (1971*a*) definition of population momentum (hence the subscript K on SER). This, in turn, is a special case of population inertia (Schoen and Kim 1991, Tuljapurkar and Lee 1997, Schoen and Jonsson 2003, Keyfitz and Caswell 2005). Our derivation of Eq. 8 (see Appendix A) does not require the assumption $\lambda_1 = 1$, but the equivalent end result is interesting. In the remainder of this paper we focus on the SER and henceforth, we use the terms "population inertia" and SER interchangeably.

Sensitivity of population inertia to changes in vital rates

The projection matrix $\mathbf{A}$ may represent the single set of focal vital rates, or, following a demographic transition, $\mathbf{A}$ may represent the set of post-transition vital rates. In both cases, one might be interested in the question: "how would population inertia change if the vital rates were just a little bit different?" To answer this question a measure for the sensitivity of population inertia to change in the underlying vital rates (a_{ij}) of the transition matrix $\mathbf{A}$ is needed.

To develop general formulas for such a sensitivity measure, we begin with Eq. 8 because this form of the SER should be most familiar to readers (e.g., presented as an equation for the more familiar population momentum in Caswell [2001] and Keyfitz and Caswell [2005]). To begin, we apply the product rule to differentiate Eq. 8 with respect to a single vital rate a_{ij}:

$$\frac{\partial \mathrm{SER}}{\partial a_{ij}} = \frac{\partial}{\partial a_{ij}} \left\{ \frac{\mathbf{e}^\top [(\mathbf{v}_1^* \mathbf{n}_0)\mathbf{w}_1]}{\mathbf{e}^\mathrm{T} \mathbf{n}_0} \right\}$$

$$= \frac{1}{\mathbf{e}^\top \mathbf{n}_0} \left\{ \mathbf{e}^\top \left[(\mathbf{v}_1^* \mathbf{n}_0) \frac{\partial \mathbf{w}_1}{\partial a_{ij}} + \left(\frac{\partial \mathbf{v}_1^*}{\partial a_{ij}} \mathbf{n}_0 \right) \mathbf{w}_1 \right] \right\}. \tag{10}$$

It becomes apparent that perturbation of a vital rate causes change in the right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors; i.e., the vectors describing stable population structure and reproductive value, respectively. Conveniently, Caswell (1980, 2001) presented formulas for sensitivities of these eigenvectors to change in a vital rate a_{ij}:

$$\frac{\partial \mathbf{w}_1}{\partial a_{ij}} = w_j^{(1)} \sum_{m\neq 1}^{n} \frac{\overline{v}_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m \tag{11}$$

$$\frac{\partial \mathbf{v}_1}{\partial a_{ij}} = v_i^{(1)} \sum_{m\neq 1}^{n} \frac{\overline{w}_j^{(m)}}{\overline{\lambda}_1 - \overline{\lambda}_m} \mathbf{v}_m. \tag{12}$$

where $w_j^{(m)}$ is the jth entry of $\mathbf{w}_m$ and $v_i^{(m)}$ is the ith entry of $\mathbf{v}_m$. Eqs. 11 and 12 are demographic applications of well-known matrix theory (Wilkinson 1988), and when incorporated into Eq. 10, the sensitivity of the SER to change in a vital rate can be seen as

$$\frac{\partial \mathrm{SER}}{\partial a_{ij}} = \frac{1}{\mathbf{e}^\top \mathbf{n}_0} \times \left[\mathbf{e}^\top \left((\mathbf{v}_1^* \mathbf{n}_0) \left[w_j^{(1)} \sum_{m\neq 1}^{n} \frac{\overline{v}_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m \right] + \left\{ \left[v_i^{(1)} \sum_{m\neq 1}^{n} \frac{\overline{w}_j^{(m)}}{\overline{\lambda}_1 - \overline{\lambda}_m} \mathbf{v}_m \right]^* \mathbf{n}_0 \right\} \mathbf{w}_1 \right) \right]. \tag{13}$$

Thus, change in a vital rate causes change in the stable population vector $\mathbf{w}_1$ and reproductive value vector $\mathbf{v}_1$, which then leads to change in the SER. Because it is not mathematically intuitive that Eq. 13 holds true, as asserted, we provide a detailed proof in Appendix B.

Sometimes matrix-level entries are computed from multiple lower-level vital rates. For example, projection-matrix fertilities are the product of fecundity and some component of survival. Sensitivity of the SER to a lower-level parameter x can be found using the chain rule:

$$\frac{\partial \mathrm{SER}}{\partial x} = \sum_{k,l} \left(\frac{\partial \mathrm{SER}}{\partial a_{kl}} \right) \left(\frac{\partial a_{kl}}{\partial x} \right). \tag{14}$$

SER sensitivities can also be calculated numerically:

$$\frac{\partial \mathrm{SER}}{\partial a_{ij}} \doteq \frac{\mathrm{SER}_{\mathrm{post}} - \mathrm{SER}_{\mathrm{pre}}}{\Delta_{ij}} \tag{15}$$

where $\mathrm{SER}_{\mathrm{pre}}$ and $\mathrm{SER}_{\mathrm{post}}$ are the measurements of population inertia before and after the instantaneous change Δ_{ij} in the vital rate a_{ij} (the "$\doteq$" symbol means "approaches in the limit"). Although we have chosen to focus on sensitivity of the SER to absolute change in vital rates, the elasticity of the SER to proportional change in vital rates can easily be calculated from the analytical sensitivity, or numerically,

$$\frac{\partial \log \mathrm{SER}}{\partial \log a_{ij}} = \left(\frac{\partial \mathrm{SER}}{\partial a_{ij}} \right) \left(\frac{a_{ij}}{\mathrm{SER}} \right) \tag{16}$$

$$\frac{\partial \log \mathrm{SER}}{\partial \log a_{ij}} \doteq \left(\frac{\mathrm{SER}_{\mathrm{post}} - \mathrm{SER}_{\mathrm{pre}}}{\mathrm{SER}_{\mathrm{pre}}} \right) \left(\frac{a_{ij}}{\Delta_{ij}} \right). \tag{17}$$

In Appendix B we show that the SER elasticities associated with the a_{ij} sum to zero (but not those associated with lower-level vital rates).

Sensitivity of population inertia to changes in population structure

Population inertia also depends on the initial population vector $\mathbf{n}_0$, and one may be interested in how direct changes in initial population structure cause change in population inertia, noting that the "initial" point in time can simply be defined as the point in time from which the population will be studied forward. To develop general formulas for this sensitivity we begin by applying the quotient rule to differentiate Eq. 8 with respect to a single entry $n_i(0)$ of the initial population vector:

$$\frac{\partial \mathrm{SER}}{\partial n_i(0)} = \mathbf{e}^\top \mathbf{w}_1 \frac{\partial}{\partial n_i(0)} \left(\frac{\mathbf{v}_1^* \mathbf{n}_0}{\mathbf{e}^\top \mathbf{n}_0} \right)$$

$$= \mathbf{e}^\top \mathbf{w}_1 \left\{ \frac{\mathbf{e}^\top \mathbf{n}_0 [\bar{v}_i^{(1)}] - \mathbf{v}_1^* \mathbf{n}_0}{(\mathbf{e}^\top \mathbf{n}_0)^2} \right\}. \qquad (18)$$

We assume for the rest of this section that $||\mathbf{n}_0|| = 1$, which allows simplification of Eq. 18:

$$\frac{\partial \mathrm{SER}}{\partial n_i(0)} = v_i^{(1)} - \mathbf{v}_1^\top \mathbf{n}_0. \qquad (19)$$

In particular, if one examines the special case where $\mathbf{n}_0 = \mathbf{w}_1$, then

$$\left. \frac{\partial \mathrm{SER}}{\partial n_i(0)} \right|_{\mathbf{w}_1} = v_i^{(1)} - 1. \qquad (20)$$

Thus, to apply Eq. 19, knowledge of only the reproductive value and initial population structure are needed to measure the sensitivity of the SER to change in a single entry of the initial population structure. If it is safe to assume that the population structure is initially stable (Eq. 20), then only reproductive value is needed, which is easily computed from **A**.

Environmental and anthropogenic perturbations to population structure will rarely affect just a single (st)age class. Thus, to provide population inertia sensitivities for more realistic applications, we now consider the case where a perturbation affects multiple (st)age classes simultaneously. To do this, let $\mathbf{u} = [u_1, \ldots, u_n]^\top$ be an arbitrary unit vector (i.e., $||\mathbf{u}|| = 1$) to be regarded as a perturbation vector applied to $\mathbf{n}_0$. Furthermore, denote by $D_\mathbf{u}\mathrm{SER}$ the directional derivative of SER in the direction **u**. Then,

$$D_\mathbf{u}\mathrm{SER} = \nabla \mathrm{SER}^\top \mathbf{u} \qquad (21)$$

where $\nabla \mathrm{SER} = [\partial \mathrm{SER}/\partial n_1(0), \ldots, \partial \mathrm{SER}/\partial n_n(0)]^\top$ is the gradient of the SER. The set of all vectors **x** for which $\nabla \mathrm{SER}^\top \mathbf{x} = 0$ forms a hyperplane in n-space. The set of those **x** for which $\nabla \mathrm{SER}^\top \mathbf{x} > 0$ (respectively, $\nabla \mathrm{SER}^\top \mathbf{x} < 0$) are on the positive side (respectively, negative side) of the hyperplane. Thus, the directional derivative is positive, negative, or zero when **u** is on the positive side of the hyperplane, the negative side, or in the hyperplane itself, respectively.

Considering the special case where $\mathbf{n}_0 = \mathbf{w}_1$ (with each being a unit vector), we get

$$D_\mathbf{u}\mathrm{SER}|_{\mathbf{w}_1} = \nabla \mathrm{SER}^\top \mathbf{u}$$

$$= (\mathbf{v}_1 - \mathbf{e})^\top \mathbf{u}. \qquad (22)$$

In this case, the SER equals 1. Therefore, the new value of population inertia after perturbation is >1, <1, or =1 when the directional derivative is >0, <0, or =0, respectively. If $\mathbf{u} = \mathbf{w}_1$, then the distribution of individuals among stage classes does not change following the perturbation (**u**), so the SER is expected to remain at 1. This is indeed the case, since

$$D_{\mathbf{w}_1}\mathrm{SER}|_{\mathbf{w}_1} = (\mathbf{v}_1 - \mathbf{e})^\top \mathbf{w}_1 = \mathbf{v}_1^\top \mathbf{w}_1 - \mathbf{e}^\top \mathbf{w}_1$$

$$= \mathbf{v}_1^\top \mathbf{w}_1 - 1 = 0.$$

APPLICATIONS AND EXAMPLES

Age-related dynamics of inertia in a population open to migration

Nearly all studies of population inertia in demography have focused on momentum following change in fertility to the stationary level. Yet, changes in age-structured vital rates other than fertility are expected to produce population inertia and warrant more study (Li and Tuljapurkar 1999). In addition to fertility and survival, dynamics of "open" populations are affected by immigration and emigration, which can significantly affect population inertia (Rogers and Willekens 1978, Rogers 1995). Here, we provide an example using data for a female segment of the U.S. population <50 years old (Rogers 1995) to illustrate how our formulae can be used to examine the elasticity of population inertia to changes in age-specific (or stage-specific) vital rates of an open population. We assumed that the population initially had a stable population structure and applied Eqs. 13, 14, and 16 to calculate and compare the elasticity of SER to changes in age-specific survival, fecundity, immigration probability, and local population fidelity (the complement of emigration probability). Details of the population model and data are provided in Appendix C. The Supplement contains Matlab scripts for conducting this example.

Interestingly, the elasticity of SER to changes in age-specific survival, fidelity (η_x), and immigration changed from negative to positive values with increasing age. Meanwhile, elasticities for fecundity were always negative indicating that increased fecundity always created inertia leading to smaller population size relative to an otherwise equivalent population in its stable population structure (Fig. 2). (We note that elasticity values indicate results for an increase in a vital rate, and decreases

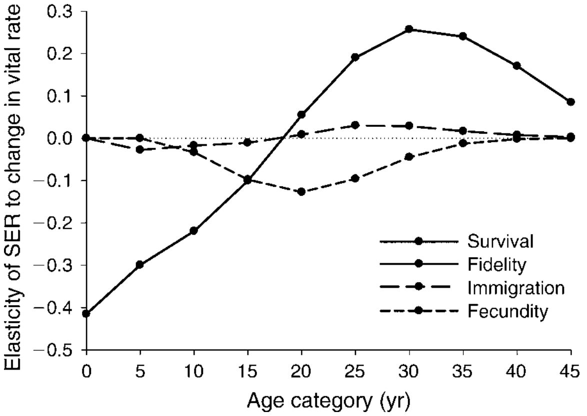

FIG. 2. Elasticity of the stable equivalent ratio (SER) to changes in survival probability, local population fidelity, immigration probability, and fecundity across age categories for the U.S. Southwest population example (see *Applications and Examples*). Note that the elasticity values for survival and fidelity are exactly the same.

would produce exactly the opposite result. We also note that elasticities for survival probabilities and fidelity were identical because of their perfect multiplicative relation in the model; Appendix C.) The effect of changing a vital rate on the stable population structure and reproductive value (see Eq. 13) varied with age, leading to the patterns in SER elasticities across age (Fig. 2). Furthermore, changes in fecundity did not have the largest impact on the SER, changes in survival and local population fidelity did. Thus, while demographers seem to be quite concerned about the effects of the contemporary fertility transition on population momentum (see numerous citations in *Introduction*), perhaps they should also be concerned about the effects of increasing longevity (sensu Guillot 2005) and changes in migration rates on population inertia. Moreover, population inertia could also have profound impacts on the economy (Lee 2000) and use of natural resources (Liu et al. 1999, 2003) because of its effects on the abundance of specific age groups, e.g., age groups in the working force or elderly dependents. Hence, age-specific patterns in SER elasticities (see Fig. 2) could be very important in these areas of study as well.

Our formulae can also be applied to models that explicitly treat spatial population structure (e.g., multiregional populations; Rogers 1995). In Appendix D we provide an example illustrating how population inertia sensitivities can be used to design creative management strategies for a source–sink metapopulation (Pulliam 1988, Hanski and Gilpin 1997).

Effects of perturbing population structure in management and conservation

In many cases, managers and pest-control officials might want to consider how different management strategies focused on population structure could change population inertia in ways to achieve abundance-related management goals in a more timely and efficient manner (MacArthur 1960, Merrill et al. 2003, Koons et al. 2006*b*). Plant and animal stocking programs (e.g., captive release or relocation of wild individuals) provide managers a variety of ways to directly add individuals to specific age or stage classes of a population (e.g., Starling 1991, Wolf et al. 1996, Ostermann et al. 2001), while harvest, live-trapping, and other removal techniques allow managers to directly decrease abundance in certain stage classes (Larkin 1977, Holt and Talbot 1978). All of these management practices will affect population structure. If goals are very short-term and management is implemented frequently (e.g., every year), then transient sensitivities of population abundance, growth rate, reactivity, and other dynamics (see Caswell 2007) will be very useful in guiding short-term management decisions. If management is not applied as frequently, then the effects of the abovementioned management practices on population inertia could help managers make better decisions to achieve their goals (see also Appendix D).

For such cases, we provide a hypothetical example that illustrates how population inertia is affected by direct management perturbations to population structure. The following matrix **A** describes fertility and survival probabilities of striped bass (*Morone saxatilis*) (Cohen et al. 1983):

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & 0 & 5.25 \times 10^{4} \\ 1.24 \times 10^{-5} & 0 & 0 & 0 \\ 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0.6 & 0.6 \end{bmatrix}.$$

A is constructed in the traditional post-breeding census format (Caswell 2001), adult fertility is in the upper right corner of the matrix, and survival probabilities are on the sub-diagonal and bottom-right corner. The first age class represents small offspring (small fry), the second and third represent subadults, and the fourth represents all adults.

In the long run, a population of striped bass experiencing the vital rates in **A** would decrease by 9% each year ($\lambda_1 = 0.91$). This occurs in commercial or sport fisheries when harvest (or other factors) reduces survival chances to levels that cannot be compensated by reproductive output. To alleviate the continual depreciation of a fishery, managers often use stocking programs to replenish populations of striped bass (Sutton et al. 2000) and other species. Here, we see if population inertia sensitivities to direct changes in population structure (i.e., the very action of stocking) can motivate ways to improve the efficiency of stocking efforts to increase abundance, and potentially reduce the frequency of stocking required to maintain the fishery.

To begin, we calculated the dominant left $\mathbf{v}_1 = [0.17, 1.25 \times 10^{4}, 1.88 \times 10^{4}, 2.85 \times 10^{4}]^{\top}$ and right $\mathbf{w}_1 = [0.9996, 1.36 \times 10^{-5}, 8.97 \times 10^{-6}, 1.73 \times 10^{-5}]^{\top}$ eigenvectors of **A**. We assumed that population structure was initially stable (i.e., $\mathbf{n}_0 \propto \mathbf{w}_1$), indicating SER

TABLE 1. The sensitivity of population inertia to unit changes $\mathbf{u}$ in the initial population structure of the example population of striped bass, indicated by the directional derivative $D_{\mathbf{u}}\mathrm{SER}|_{\mathbf{w}_1}$.

$\mathbf{u}$†	$D_{\mathbf{u}}\mathrm{SER}|_{\mathbf{w}_1}$
$[1, 0, 0, 0]^\top$	−0.83
$[0, 1, 0, 0]^\top$	1.24×10^4
$[0, 0, 1, 0]^\top$	1.88×10^4
$[0, 0, 0, 1]^\top$	2.85×10^4
$[0.25, 0.25, 0.25, 0.25]^\top$	1.49×10^4
$[0.75, 0.25, 0, 0]^\top$	3.09×10^3
$[0.99, 0, 0, 0.01]^\top$	284.20
$[0.99996, 1.36 \times 10^{-5}, 8.97 \times 10^{-6}, 1.73 \times 10^{-6}]^\top$‡	0

Note: We used the dominant left eigenvector $\mathbf{v}_1 = [0.17, 1.24 \times 10^4, 1.88 \times 10^4, 2.85 \times 10^4]^\top$ and the following gradient of the SER (stable equivalent ratio): $\nabla\mathrm{SER} = [-0.83, 1.24 \times 10^4, 1.88 \times 10^4, 2.85 \times 10^4]^\top$, each rounded to the second decimal.

† Unit decreases produce exactly the opposite result.

‡ The stable population structure rounded to the second decimal.

initially = 1. Then, we used the directional derivative in Eq. 22 to calculate the sensitivity of SER to perturbations in population structure. The units of increase (or decrease) refer to individuals.

If only the ith entry of initial population structure is perturbed, then the direction SER moves away from 1 is dictated by the sign of the ith entry of $\nabla\mathrm{SER}$: $v_i^{(1)} - 1$. For example, a unit increase in the first stage class decreases population inertia ($D_{\mathbf{u}}\mathrm{SER}|_{\mathbf{w}_1} = -0.83$). A unit increase in subadult stages increase population inertia substantially (unit decreases would produce exactly the opposite results), and the maximal effect on population inertia results from a unit increase in the adult stage ($D_{\mathbf{u}}\mathrm{SER}|_{\mathbf{w}_1} = 2.85 \times 10^4$). Unit perturbations that are spread across stages have intermediate effects on population inertia (see Table 1). Although perturbations equal to the stable population structure ($\mathbf{w}_1$) might increase absolute abundance, they have no effect on population inertia ($D_{\mathbf{u}}\mathrm{SER}|_{\mathbf{w}_1} = 0$, SER still equals 1 following perturbation).

These results might be very useful in designing better stocking programs. For illustration, consider a scenario where stocking occurs once the population drops to a unit of individuals, at which time the manager stocks an additional unit to the population. Release of small fry is a common stocking practice for striped bass (Sutton et al. 2000) and many other species; however, releasing a unit of small fry will disrupt population structure in a way that decreases population inertia and would result in long-term abundance that is just 17% of that for a release that is made proportional to $\mathbf{w}_1$. As a result, stocking would have to be done 5.6 times more frequently than a stocking program done in proportion to $\mathbf{w}_1$ (Fig. 3a), which for striped bass, would constitute releasing just a small number of subadults and adults relative to the number of small fry released (Table 1). Releasing a unit of adults on the other hand would produce maximal population inertia, a long-term

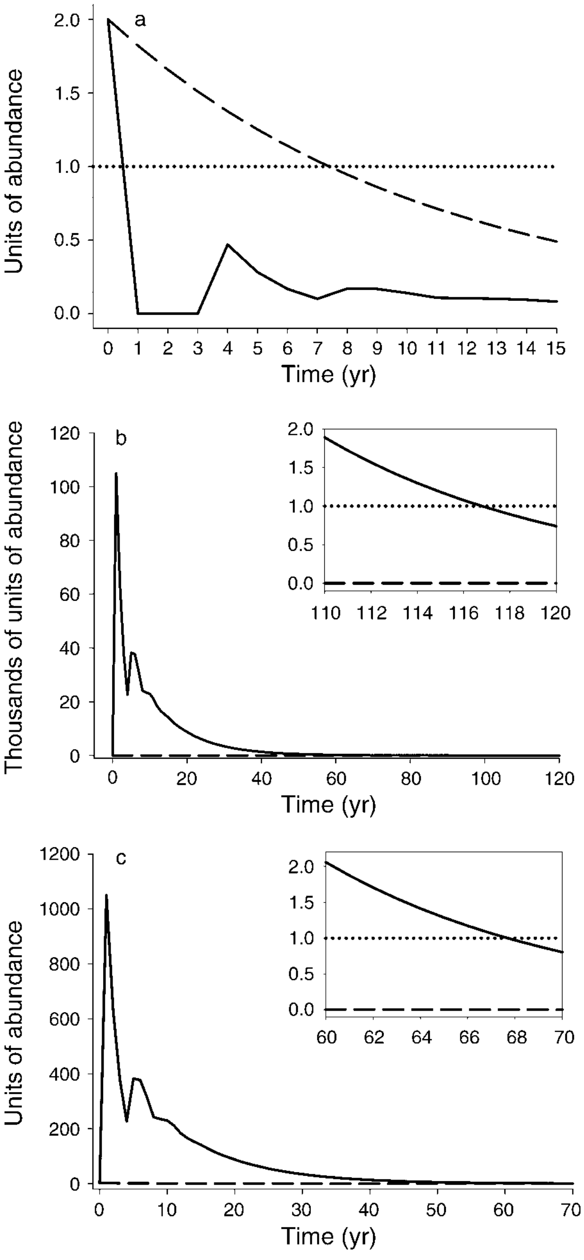

FIG. 3. Transient dynamics and population inertia resulting from stocking one unit of individuals (10, 1000, and so on; results are not affected by the chosen number) for populations of striped bass that were in a stable population structure $\mathbf{w}_1$ and had dropped to a single unit (thus, projections begin with a total of two units). Projections are for (a) stocking a unit of fry (solid line) relative to stocking made in proportion to $\mathbf{w}_1$ (always the dashed line); (b) stocking a unit of adults (solid line) relative to stocking made in proportion to $\mathbf{w}_1$; (c) stocking one adult for every 99 fry (solid line) relative to stocking made in proportion to $\mathbf{w}_1$. Note differences in the time elapsed until the population drops to a single unit (dotted line), at which time managers would have to release another unit of individuals.

abundance that is 2.85×10^4 times greater than that for a program where release is conducted in proportion to $\mathbf{w}_1$, and duration between stocking would be increased 14 times (presumably a very good thing; Fig. 3b). If this management practice were too expensive, release of just one adult for every 99 fry would still lead to a substantial increase in population inertia (Table 1), and duration between stocking would be increased 8.18 times relative to a release proportional to $\mathbf{w}_1$ (Fig. 3c) and 45.8 times relative to a pure release of small fry. Apart from the effects of perturbation to structure on population inertia, each scenario also resulted in a very large transient reaction to the perturbation (see Figs. 1 and 3), which might be of more interest to a manager if goals are very short-term (see Caswell 2007 for transient sensitivities). The Supplement contains a Matlab script for conducting this example, and includes code for randomly selecting a perturbation vector from a simplex that might be useful for examining situations where perturbations cannot be perfectly controlled (e.g., harvest).

In general, the influence of population structure on eventual population size is of great importance in conservation biology and management (Keyfitz and Caswell 2005). When stocking or reintroducing species into previously habited areas, it would be most effective to introduce individuals of an age and reproductive value that would maximize the SER, or at least improve upon an existing management program. Similarly, invasion of nonnative plants and animals can lead to substantial economic and environmental damage. Management aimed at minimizing the SER would be of interest in the control of invasive species (Keyfitz and Caswell 2005, Koons et al. 2006*b*) and our formulae could help refine management agendas in both situations. The particular effect of a perturbation on the transient dynamics and inertia of a population will depend on the organism's life history and the way in which structure is perturbed away from the stable population structure (Koons et al. 2005, 2006*a*); financial costs will limit what managers can actually do. In Appendix E, we provide another example describing the sensitivity of population inertia across life history strategies.

Discussion

Population inertia is a measure more closely related to population size than growth rate, and unlike growth rate, population size is very responsive to initial population structure (Tuljapurkar and Lee 1997). Direct or indirect (via vital rates) changes in population structure create transient dynamics having an effect on both short- and long-term size, which is an issue that is best addressed with formal perturbation measures like sensitivities. Analytical sensitivities have been developed for population size (Fox and Gurevitch 2000, Yearsley 2004, Caswell 2007). However, we have drawn upon matrix theory (Wilkinson 1988) to derive a suite of sensitivity formulae for the SER. These formulae differ from those for population size itself because the SER is a ratio measuring the inertial effects of population structure and transient dynamics on long-term population size relative to an otherwise equivalent population in its asymptotically stable population structure.

Most often, demographers and population biologists focus on asymptotic measures of population dynamics (e.g., r, λ_1) making the SER especially useful because it provides a direct comparison of the actual dynamics resulting from changes in the vital rates and population structure to the asymptotic population dynamics (Fig. 1). Thus, SER sensitivities can readily be used to examine the consequences of assuming a stable population structure, which is common practice. Furthermore, we have shown that SER sensitivities could be used to address a large array of new questions in human demography, conservation, natural resource management, and comparative life history analysis.

For example, human demographers usually study population inertia resulting from changes in fertility (see *Introduction*). By using our formulas and considering all vital rates constituting a population open to migration, we found changes to age-specific survival and emigration probabilities to have a greater proportionate effect on population inertia than changes in fertility. In the context of human populations, such results could be important in the development of socio-demographic policies (Guillot 2005). In the context of wild organisms, population inertia affects the long-term population trajectory, and could thus shorten or lengthen the time it takes for a population to go extinct, recover from depletion, or grow to levels that become a nuisance (Koons et al. 2006*b*). Conservationists often focus directly on improving asymptotic growth rate in sink populations (i.e., populations where $\lambda_1 < 1$). In cases where this is not economically feasible, we have shown that SER sensitivities can motivate alternatives for the management of spatially structured source–sink populations. Infrequent management of corridors to improve dispersal from a (potentially density-regulated) source to a sink can have interesting effects on population inertia that can increase long-term abundance in a sink and the overall metapopulation; even without affecting asymptotic growth rates (Appendix D). In a variety of spatial situations, SER sensitivities could therefore be useful for examining the effects of change in birth, immigration, death, and emigration rates on population inertia and long-term abundance.

In another example, we discovered that SER sensitivities follow a general life history pattern related to generation length (Appendix E). Populations of long-lived species are more likely to experience large magnitudes of population inertia following a vital-rate perturbation than short-lived species, which could be extremely useful when designing general policies and management schemes to safeguard declining populations from going extinct and when trying to manage or "control" the abundance of populations experiencing surplus rates of growth (i.e., $\lambda_1 > 1$; e.g., Merrill et al. 2003, Hauser et al. 2006, Koons et al. 2006*a*, *b*).

Depending on the conservation or management situation, direct addition to, or removal from, the population may be more relevant than perturbation of vital rates (e.g., stocking and relocation programs). In our example of striped bass stocking, we made use of the gradient vector and directional derivative to show that the net inertial effect of perturbing population structure depends on (1) the stage classes that are targeted and (2) whether the perturbation increases or decreases the relative abundance in a given stage. Depending on which stage(s) are stocked (or removed), population abundance can experience enormous transient increase (or decrease) following direct perturbations to population structure (Fig. 3). In the case of harvest management, management is applied frequently (e.g., every year) and this transient "reaction" to a perturbation (Caswell and Neubert 2005) might be of more interest than the longer-term effects of population inertia. While it may be possible to control population abundance "or" inertia of a structured population with an optimal harvest strategy, it is not feasible to simultaneously control both because of the fluctuating nature of transient dynamics (sensu Hauser et al. 2006). Thus, examination of transient reactions to perturbations might be of more use in harvest management (Caswell 2007). On the other hand, stocking, relocation, and reintroduction programs might involve less frequent application of management (sometimes once). In these cases, the inertial effects of direct perturbation to population structure on long-term abundance will be of great interest because it can aid the design of more efficient management practices in terms of both population dynamics and finances (see example above). In any event, perturbations to population structure have important effects on transient dynamics (Koons et al. 2005, Mertens et al. 2006) and long-term abundance, which are both of management and conservation concern.

Formulas relating change in demographic parameters to change in the asymptotic population growth rate (e.g., Caswell 1978), transient dynamics (Fox and Gurevitch 2000, Yearsley 2004, Koons et al. 2005, Mertens et al. 2006, Caswell 2007), and inertia in long-term population size (here) are all needed to better understand population dynamics from evolutionary and applied points of view. Our work provides a way to more deeply study the latter, and provides a template for generalizing our formulae to situations where populations might be affected by environmental variability (see Tuljapurkar and Lee 1997) as well as their own density. Our formulae can be used to approximate the sensitivity of population inertia to changes in vital rates and population structure for density-regulated populations that are either at low density or near an equilibrium (see Appendix D). Nevertheless, we encourage generalizations of our results and think that Caswell's (2007) introduction of matrix calculus into demography and ecology will be very useful for expanding our formulae to all density-regulated populations and those inhabiting changing environments. The latter of which could also be a way to examine the effects of frequent management (e.g., harvest) or gradual policy change on population inertia.

Acknowledgments

The authors thank H. Caswell, R. F. Rockwell, and two anonymous reviewers for discussion and comments on an earlier version of this paper. D. N. Koons and J. B. Grand appreciate the support of D. V. Derksen and Lyman K. Thorsteinson of USGS, Biological Resources Division. This research addresses a priority identified by the Minerals Management Service, Alaska Outer Continental Shelf Region. The USGS, Biological Resources Division, Alaska Biological Science Center funded this research. D. N. Koons was supported by a Max Planck Society postdoctoral fellowship in the final stages of this research. D. N. Koons and R. R. Holmes contributed equally to this manuscript.

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.

Bongaarts, J., and R. A. Bulatao. 1999. Completing the demographic transition. Population and Development Review 25:515–529.

Bos, E., M. T. Vu, E. Massiah, and R. A. Bulatao. 1994. World population projections 1994–1995: Estimates and projections with related demographic statistics. John Hopkins University Press, Baltimore, Maryland, USA.

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. 1980. On the equivalence of maximizing reproductive value and maximizing fitness. Ecology 61:19–24.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H. 2007. Sensitivity analysis of transient population dynamics. Ecology Letters 10:1–15.

Caswell, H., and M. G. Neubert. 2005. Reactivity and transient dynamics of discrete-time ecological systems. Journal of Difference Equations and Applications 11:295–310.

Caughley, G. 1977. Analysis of vertebrate populations. Wiley, New York, New York, USA.

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.

Coale, A. J. 1972. The growth and structure of human populations: a mathematical approach. Princeton University Press, Princeton, New Jersey, USA.

Cohen, J. E., S. W. Christensen, and C. P. Goodyear. 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. Canadian Journal of Fisheries and Aquatic Sciences 40:2170–2183.

Demetrius, L. 1969. The sensitivity of population growth rate to perturbations in the life cycle components. Mathematical Biosciences 4:129–136.

Emlen, J. M. 1970. Age specificity and ecological theory. Ecology 51:588–601.

Fischer, G., and G. K. Heilig. 1997. Population momentum and the demand on land and water resources. Philosophical Transactions of the Royal Society of London, B 352:869–889.

Fisher, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford, UK.

Fox, G. A., and J. Gurevitch. 2000. Population numbers count: tools for near-term demographic analysis. American Naturalist 156:242–256.

Frauenthal, J. C. 1975. Birth trajectory under changing fertility conditions. Demography 12:447–454.

Gantmacher, F. R. 1959. Matrix theory. Chelsea Publishing Company, New York, New York, USA.

Goldstein, J. R. 2002. Population momentum for gradual demographic transitions: an alternative approach. Demography 39:65–73.

Goodman, L. A. 1968. An elementary approach to the population projection-matrix, to the population reproductive value, and to related topics in the mathematical theory of population growth. Demography 5:382–409.

Goodman, L. A. 1971. On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. Theoretical Population Biology 2:339–354.

Guillot, M. 2005. The momentum of mortality change. Population Studies 59:283–294.

Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology 12:12–45.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Hauser, C. E., E. G. Cooch, and J.-D. Lebreton. 2006. Control of structured populations by harvest. Ecological Modelling 196:462–470.

Heppell, S. S., C. Pfister, and H. de Kroon. 2000. Elasticity analysis in population biology: methods and applications. Ecology 81:606–606.

Holt, S. J., and L. M. Talbot. 1978. New principles for the conservation of wild living resources. Wildlife Monographs 59.

Horn, R. A., and C. R. Johnson. 1985. Matrix analysis. Cambridge University Press, Cambridge, Massachusetts, USA.

Horvitz, C. C., D. W. Schemske, and H. Caswell. 1997. The "importance" of life history stages to population growth: prospective and retrospective analyses. Pages 247–272 *in* 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*a*. On the momentum of population growth. Demography 8:71–80.

Keyfitz, N. 1971*b*. Linkages of intrinsic to age-specific rates. Journal of the American Statistical Association 66:275–281.

Keyfitz, N., and H. Caswell. 2005. Applied mathematical demography. Third edition. Springer, New York, New York, USA.

Kim, Y. J., and R. Schoen. 1997. Population momentum expresses population aging. Demography 34:421–427.

Koons, D. N., J. B. Grand, and J. M. Arnold. 2006*a*. Population momentum across vertebrate life histories. Ecological Modelling 197:418–430.

Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. Ecological Modelling 185:283–297.

Koons, D. N., R. F. Rockwell, and J. B. Grand. 2006*b*. Population momentum: implications for wildlife management. Journal of Wildlife Management 70:19–26.

Larkin, P. A. 1977. An epitaph for the concept of maximum sustained yield. Transactions of the American Fisheries Society 106:1–11.

Lee, R. D. 2000. A cross-cultural perspective on intergenerational transfers and the economic life cycle. Pages 17–56 *in* A. Mason and G. Tapinos, editors. Sharing the wealth: demographic change and economic transfers between generations. Oxford University Press, Oxford, UK.

Lewontin, R. C. 1965. Selection for colonizing ability. Pages 79–94 *in* H. G. Baker and G. L. Stebbins, editors. The genetics of colonizing species. Academic Press, New York, New York, USA.

Li, N., and S. Tuljapurkar. 1999. Population momentum for gradual demographic transitions. Population Studies 53:255–262.

Li, N., and S. Tuljapurkar. 2000. The solution of time-dependent population models. Mathematical Population Studies 7:311–329.

Liu, J., G. C. Daily, P. R. Ehrlich, and G. W. Luck. 2003. Effects of household dynamics on resource consumption and biodiversity. Nature 421:530–533.

Liu, J., Z. Ouyang, Y. Tan, J. Yang, and H. Zhang. 1999. Changes in human population structure: implications for biodiversity conservation. Population and Environment 21: 45–58.

MacArthur, R. H. 1960. On the relation between reproductive value and optimal predation. Proceedings of the National Academy of Sciences (USA) 46:143–145.

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.

Mertens, S. K., J. M. Yearsley, F. van den Bosch, and C. A. Gilligan. 2006. Transient population dynamics in periodic matrix models: methodology and effects of cyclic permutations. Ecology 87:2338–2348.

Mertz, D. B. 1971. Life history phenomena in increasing and decreasing populations. Pages 361–399 *in* G. P. Patil, E. C. Pielou, and W. E. Waters, editors. Statistical ecology. Volume 2. Pennsylvania State University Press, University Park, Pennsylvania, USA.

Mitra, S. 1976. Influence of instantaneous fertility decline to replacement level on population growth: an alternative model. Demography 13:513–519.

Ostermann, S. D., J. R. Deforge, and W. D. Edge. 2001. Captive breeding and reintroduction evaluation criteria: a case study of peninsular bighorn sheep. Conservation Biology 15:749–760.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Rogers, A. 1995. Multiregional demography: principles, methods and extensions. Wiley, New York, New York, USA.

Rogers, A., and F. Willekens. 1978. The spatial reproductive value and the spatial momentum of zero population growth. Environment and Planning A 10:503–518.

Schoen, R., and S. H. Jonsson. 2003. Modeling momentum in gradual demographic transitions. Demography 40:621–635.

Schoen, R., and Y. J. Kim. 1991. Movement towards stability as a fundamental principle of population dynamics. Demography 28:455–466.

Schoen, R., and Y. J. Kim. 1998. Momentum under a gradual approach to zero growth. Population Studies 52:295–299.

Seneta, E. 1981. Non-negative matrices and Markov chains. Second edition. Springer-Verlag, New York, New York, USA.

Sibly, R. M., J. Hone, and T. H. Clutton-Brock. 2002. Introduction to a discussion meeting issue "population growth rate: determining factors and role in population regulation." Philosophical Transactions of the Royal Society of London, B 357:1149–1151.

Starling, A. E. 1991. Workshop summary: captive breeding and release. Ornis Scandinavica 22:255–257.

Sutton, T. M., K. A. Rose, and J. J. Ney. 2000. A model analysis of strategies for enhancing stocking success of landlocked striped bass populations. North American Journal of Fisheries Management 20:841–859.

Tuljapurkar, S., and R. Lee. 1997. Demographic uncertainty and the stable equivalent population. Mathematical and Computer Modelling 26:39–56.

United Nations. 2003. World population prospects: the 2002 revision. Volume 1. United Nations. New York, New York, USA.

van Groenendael, J. M., H. de Kroon, and H. Caswell. 1988. Projection matrices in population biology. Trends in Ecology and Evolution 3:264–269.

Wachter, K. W. 1988. Age group growth rates and population momentum. Population Studies 42:487–494.

Wilkinson, J. H. 1988. The algebraic eigenvalue problem. Oxford University Press, Oxford, UK.

Wolf, C. M., B. Griffith, C. Reed, and S. A. Temple. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. Conservation Biology 10:1142–1154.

Yearsley, J. M. 2004. Transient population dynamics and short-term sensitivity analysis of matrix population models. Ecological Modelling 177:245–258.

APPENDIX A

Derivation of relationships among measures of population inertia and momentum that have appeared in the scientific literature (*Ecological Archives* E088-177-A1).

APPENDIX B

Proof of Eq. 13 and that the SER elasticities associated with the matrix entries sum to zero (*Ecological Archives* E088-177-A2).

APPENDIX C

Technical details of the example depicting age-related dynamics of inertia in a human population open to migration (*Ecological Archives* E088-177-A3).

APPENDIX D

An example illustrating population inertia sensitivities in a source–sink metapopulation (*Ecological Archives* E088-177-A4).

APPENDIX E

An example illustrating population inertia sensitivities across life history strategies (*Ecological Archives* E088-177-A5).

SUPPLEMENT

Matlab files for conducting applications and examples (*Ecological Archives* E088-177-S1).