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POPULATION INERTIA AND ITS SENSITIVITY TO CHANGES IN VITAL RATES OR INITIAL CONDITIONS

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Abstract. Many studies have examined Keyfitz's population momentum, a special case of inertia in long-term population size resulting from demographic transition to the stationary population growth rate. Yet, population inertia can be produced by any demographic perturbation (i.e., not just perturbations that produce stationary growth). Insight into applied population dynamics, population ecology, and life history evolution has been gained using perturbation analysis of the population growth rate. However, a similar, generalized framework for perturbation analysis of population inertia has not been developed. We derive general formulas for the sensitivity of population inertia to change in any vital rate or initial population structure. These formulas are readily computable, and we provide examples of their potential use in life history and applied studies of populations.

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

1. 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, size, sex, or other phenotypic categories) because it greatly simplifies study of how underlying vital rates, such as fecundity and survival, affect population size and growth. Yet, if a population has an unstable population structure, such as an 'over abundance' of mature adults, it will experience transient dynamics (i.e., unstable short-term dynamics; Coale 1972, Fox and Gurevitch, 2000; Koons et al., 2005; Yearsley, 2004). Unstable population structure and transient dynamics can in turn create an inertial effect on long-term population size causing it to be larger or smaller than that of a population of the same initial size but with stable population structure and growing according to the same vital rates (Tuljapurkar and Lee, 1997). The most commonly studied case of population inertia is Keyfitz's heralded concept of population momentum (1971a), 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. 1).

Because population size can affect a variety of political, social, and economic issues, population momentum has been studied extensively in human demography and its effect has been shown to occur in many populations (e.g., Keyfitz, 1971a; Frauenthal, 1975; Mitra, 1976; Wachter, 1988; Schoen and Kim, 1991; Fischer and Heilig, 1997; Kim and Schoen, 1997; Schoen and Kim, 1998; Bongaarts and Bulatao, 1999; Li and Tuljapurkar, 1999, 2000; Goldstein 2002; Schoen and Jonsson, 2003). Through

simulation, biologists have recently shown that population momentum could affect conservation efforts of declining wild populations and control of pest populations (Koons et al., 2006a), that it varies with life history in a predictable pattern (Koons et al., 2006b), and that it is an important aspect of optimal harvest theory (Hauser et al., 2006).

Like population growth rate, population inertia is as relevant to population biology as it is to classical human demography, and tools that relate change in underlying demographic parameters to change in population inertia could benefit a variety of demographic disciplines. 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 1971b, 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 would be just as useful, but have not been developed. Here, we present such formulae for the sensitivity of population inertia to changes in any vital rate or initial conditions. We then show how these formulae can be used to examine dynamic underpinnings of population inertia across life histories, and in applied population analysis.

2. DERIVATION

2.1. Population Model And Notation

We use bold-type capital letters to denote matrices and bold-type lower case letters to denote vectors. We use $\bar{x}$ to denote the conjugate of x, $\mathbf{x}^{\mathrm{T}}$ to denote the transpose of the vector $\mathbf{x}$ and $\mathbf{x}^*$ to denote the complex conjugate transpose.

Most studies of population inertia are conducted with continuous time models. However, the underlying mechanisms of population inertia are more easily seen in discrete form (Schoen and Jonsson, 2003). Thus, our derivation is based on a linear, discrete, time-invariant 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 $i \neq j$.

The 1-norm of the vector $\mathbf{x}$ is given by $\|\mathbf{x}\| = \sum_{i=1}^{n} x_i$, where x_i is the ith component of x.

2.2. Measurement Of Population Inertia

In a deterministic environment, population inertia is defined as the long-term size of a population growing at any rate as determined by the actual population structure, relative to the size of an otherwise equivalent population that grows according to its stable population structure (Fig. 1b). In demography, this ratio is known as the Stable Equivalent Ratio (SER; sensu Tuljapurkar and Lee, 1997). In order to relate various notions of population inertia and momentum that have appeared in the literature, we consider the quantity

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

which we call the "inertia 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". Since

$$\frac{\|\mathbf{n}_t\| \|\mathbf{r}_0\|}{\|\mathbf{r}_t\| \|\mathbf{n}_0\|} = \frac{\left\| \mathbf{A}^t \dfrac{\mathbf{n}_0}{\|\mathbf{n}_0\|} \right\|}{\left\| \mathbf{A}^t \dfrac{\mathbf{r}_0}{\|\mathbf{r}_0\|} \right\|}, \tag{6}$$

one can see that $M_{\mathbf{r}_0}$ is the asymptotic ratio of the size of the population with initial

structure $\mathbf{n}_0$ normalized to a unit vector to that with initial structure $\mathbf{r}_0$ normalized to a

unit vector. Note that $M_{\mathbf{r}_0}$ depends only on the line determined by $\mathbf{r}_0$, that is,

$M_{c\,\mathbf{r}_0} = M_{\mathbf{r}_0}$ for any nonzero complex number c.

Here, we assume that the eigenvalues of $\mathbf{A}$ are indexed in such a way that

$|\lambda_1| \geq |\lambda_2| \geq \cdots \geq |\lambda_n|$. Moreover, any vector $\mathbf{x}$ can be written in the form $\mathbf{x} = \sum_{i=1}^{n} d_i \mathbf{w}_i$

for some uniquely determined complex numbers d_i. If $\mathbf{x}$ is nonzero, then d_i is nonzero

for some i and we call the least such i the "height" of $\mathbf{x}$. Note that the height of $\mathbf{x}$ is also

the least index i for which $\mathbf{v}_i^* \mathbf{x}$ is nonzero.

In Appendix 1, we establish that

$$M_{\mathbf{r}_0} = \frac{\left| \mathbf{v}_h^* \, \mathbf{n}_0 \right| \left\| \mathbf{r}_0 \right\|}{\left| \mathbf{v}_h^* \, \mathbf{r}_0 \right| \left\| \mathbf{n}_0 \right\|}, \tag{7}$$

provided $|\lambda_i| < |\lambda_h|$ for $i > h$, where h is the lesser of the height of $\mathbf{n}_0$ and the height of

$\mathbf{r}_0$ (or the common value if they are the same). The fraction is interpreted as being

infinity if the denominator is zero.

Now we consider various special cases of $M_{\mathbf{r}_0}$ that are of notable biological

interest. First, assume that $\mathbf{r}_0 = c\mathbf{w}_1$ for some positive real number c. Since, Eq. (5)

gives, in this case, the Stable Equivalent Ratio (SER) described above, we set

$\text{SER} = M_{\mathbf{r}_0} = M_{c\mathbf{w}_1}$. From remarks above, we see that this quantity does not depend on

c. Because $\mathbf{r}_0$ has height one, Eq. (7) yields

$$\text{SER} = \frac{\mathbf{v}_1^* \mathbf{n}_0 \left\| \mathbf{r}_0 \right\|}{\mathbf{v}_1^* \mathbf{r}_0 \left\| \mathbf{n}_0 \right\|} \tag{8}$$

(noting that the absolute value signs can be dropped since the vectors on the right are all

real and nonnegative). If we further assume that $\mathbf{r}_0$ is of the same size as $\mathbf{n}_0$ (i.e.,

$\left\| \mathbf{r}_0 \right\| = \left\| \mathbf{n}_0 \right\|$), then Eq. (8) reduces to

$$\text{SER} = \frac{\mathbf{v}_1^* \mathbf{n}_0}{\mathbf{v}_1^* \mathbf{r}_0}, \tag{9}$$

which is consistent with Eq. (7) in Tuljapurkar and Lee (1997).

Next, by replacing $\mathbf{r}_0$ in Eq. (8) with $c\mathbf{w}_1$ and canceling c's we get

$$\text{SER} = \frac{\mathbf{v}_1^* \mathbf{n}_0 \left\| \mathbf{w}_1 \right\|}{\mathbf{v}_1^* \mathbf{w}_1 \left\| \mathbf{n}_0 \right\|} = \frac{\mathbf{e}^\mathrm{T} \left(\mathbf{v}_1^* \mathbf{n}_0 \right) \mathbf{w}_1}{\mathbf{e}^\mathrm{T} \mathbf{n}_0}, \tag{10}$$

where $\mathbf{e}$ is the vector with each entry equal to one. This right-hand side of Eq. (10) 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

$$\text{SER}_K = \lim_{t \to \infty} \frac{\left\| \mathbf{n}_t \right\|}{\left\| \mathbf{n}_0 \right\|} \quad \left(\text{assuming } \lambda_1 = 1 \right), \tag{11}$$

which is equivalent to Keyfitz's (1971a) general 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). Caswell derives Eq. (10) from (11) making use of the assumption

$\lambda_1 = 1$. Our derivation of Eq. (10) from (5) does not require this assumption, but the

equivalent end result is interesting.

Lastly, if the initial vector $\mathbf{n}_0$ has height > 1, so that $\mathbf{v}_1^*\mathbf{n}_0 = 0$ (we momentarily relax the assumption that $\mathbf{A}$ is primitive to allow for this possibility), then the SER is zero and all that can be concluded is that the size of the population will become increasingly less significant as compared to that of a stable population growing at rate λ_1. However, the population might still be viable with, say, its structure vector approaching an eigenvector for a subdominant eigenvalue. In this case, the SER can be regarded as being too coarse a measure to distinguish between this population and one that, for instance, is moving toward extinction, which would also clearly have zero SER. We get a more refined view of inertial effects by choosing various reference vectors $\mathbf{r}_0$ in Eq. (5). For instance, if $\mathbf{n}_0$ has height $h > 1$ and we let $\mathbf{r}_0 = \mathbf{w}_h$ and assume that $|\lambda_i| < |\lambda_h|$ for $i > h$, then Eq. (7) gives

$$M_{\mathbf{r}_0} = \frac{\left|\mathbf{v}_h^*\mathbf{n}_0\right|\left\|\mathbf{w}_h\right\|}{\left\|\mathbf{n}_0\right\|} . \tag{12}$$

This inertia $M_{\mathbf{r}_0}$ is nonzero (since $\mathbf{v}_h^*\mathbf{n}_0 \neq 0$) and it gives the asymptotic size of the given population relative to the size of a stable population growing at the subdominant rate λ_h. In the remainder of this paper we focus on the SER and leave further investigation of this more general notion of inertia to future work.

The SER in Eqs. (9) and (10) can be used to measure inertia in population size caused by an initially unstable population structure, or inertia resulting from instantaneous change in any vital rate to a new level (i.e., a 'demographic transition'). For example, $\mathbf{n}_0$ can represent the initial population structure or it can represent the population structure produced by a historical set of vital rates. Of course, following a

'demographic transition', $\mathbf{v}_1$, $\mathbf{w}_1$, and $\mathbf{r}_0$ would refer to the post-transition set of vital rates. Henceforth, we use the terms 'population inertia' and SER interchangeably.

2.3. General Formulas For The Sensitivity Of Population Inertia To Changes In Vital Rates

$\mathbf{A}$ 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." 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 answer this question.

Thus, to develop general formulas for such a sensitivity measure, we begin with Eq. (10) because this form of the deterministic SER should be most familiar to readers (e.g., presented as an equation for the more familiar M in Caswell, 2001; Keyfitz and Caswell, 2005). To begin, we apply the product rule to differentiate Eq. (10) with respect to a single vital rate a_{ij}:

$$
\begin{aligned}
\frac{\partial \, \text{SER}}{\partial a_{ij}} &= \frac{\partial}{\partial a_{ij}} \left(\frac{\mathbf{e}^{\text{T}} \left[\left(\overset{*}{\mathbf{v}}_1 \mathbf{n}_0 \right) \mathbf{w}_1 \right]}{\mathbf{e}^{\text{T}} \mathbf{n}_0} \right) \\
&= \frac{1}{\mathbf{e}^{\text{T}} \mathbf{n}_0} \left[\mathbf{e}^{\text{T}} \frac{\partial}{\partial a_{ij}} \left[\left(\overset{*}{\mathbf{v}}_1 \mathbf{n}_0 \right) \mathbf{w}_1 \right] + 0 \right] \\
&= \frac{1}{\mathbf{e}^{\text{T}} \mathbf{n}_0} \left[\mathbf{e}^{\text{T}} \left[\left(\overset{*}{\mathbf{v}}_1 \mathbf{n}_0 \right) \frac{\partial \mathbf{w}_1}{\partial a_{ij}} + \left(\frac{\partial}{\partial a_{ij}} \left(\overset{*}{\mathbf{v}}_1 \mathbf{n}_0 \right) \right) \mathbf{w}_1 \right] \right] \\
&= \frac{1}{\mathbf{e}^{\text{T}} \mathbf{n}_0} \left[\mathbf{e}^{\text{T}} \left[\left(\overset{*}{\mathbf{v}}_1 \mathbf{n}_0 \right) \frac{\partial \mathbf{w}_1}{\partial a_{ij}} + \left(\frac{\partial \overset{*}{\mathbf{v}}_1}{\partial a_{ij}} \mathbf{n}_0 \right) \mathbf{w}_1 \right] \right].
\end{aligned}
\tag{13}
$$

It becomes apparent that perturbation of a vital rate causes change in the right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors. Conveniently, Caswell (1980, 2001) has developed formulas for sensitivities of these eigenvectors to change in a vital rate a_{ij}:

$$\frac{\partial \mathbf{w}_1}{\partial a_{ij}} = w_j^{(1)} \sum_{m \neq 1}^{n} \frac{\bar{v}_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m, \tag{14}$$

$$\frac{\partial \mathbf{v}_1}{\partial a_{ij}} = v_i^{(1)} \sum_{m \neq 1}^{n} \frac{\bar{w}_j^{(m)}}{\bar{\lambda}_1 - \bar{\lambda}_m} \mathbf{v}_m. \tag{15}$$

where $w_j^{(m)}$ is the jth entry of $\mathbf{w}_m$ and $v_i^{(m)}$ is the ith entry of $\mathbf{v}_m$. By incorporating Caswell's formulas (our Eqs. 14 and 15) into Eq. (13), the sensitivity of the deterministic SER to change in a vital rate can be seen as

$$\frac{\partial \, \text{SER}}{\partial a_{ij}} = \frac{1}{\mathbf{e}^{\text{T}} \mathbf{n}_0} \left[\mathbf{e}^{\text{T}} \left[\left(\mathbf{v}_1^* \mathbf{n}_0 \right) \left(w_j^{(1)} \sum_{m \neq 1}^{n} \frac{\bar{v}_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m \right) + \left(\left(v_i^{(1)} \sum_{m \neq 1}^{n} \frac{\bar{w}_j^{(m)}}{\bar{\lambda}_1 - \bar{\lambda}_m} \mathbf{v}_m \right)^* \mathbf{n}_0 \right) \mathbf{w}_1 \right] \right]. \tag{16}$$

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. In appendix 2, we prove that Eqs. (14) and (15) can indeed be incorporated into Eq. (13) to yield (16).

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. The sensitivity of population inertia to a lower-level parameter x can be found using the chain rule

$$\frac{\partial \, \text{SER}}{\partial x} = \sum_{k,l} \frac{\partial \, \text{SER}}{\partial a_{kl}} \frac{\partial a_{kl}}{\partial x}. \tag{17}$$

Population inertia sensitivities can also be calculated numerically

$$\frac{\partial \, \text{SER}}{\partial a_{ij}} \doteq \frac{\text{SER}_{post} - \text{SER}_{pre}}{\Delta_{ij}}. \tag{18}$$

Here, SER_{pre} and SER_{post} are the measurements of population inertia before and after

the instantaneous change Δ_{ij} in the vital rate a_{ij}. Although we have chosen to focus on

the sensitivity of population inertia to absolute change in vital rates, the elasticity of

population inertia to proportional change in vital rates can easily be calculated from the

analytical sensitivity or numerically,

$$\frac{\partial \log \text{SER}}{\partial \log a_{ij}} = \frac{\partial \, \text{SER}}{\partial a_{ij}} \frac{a_{ij}}{\text{SER}} \tag{19}$$

$$\frac{\partial \log \text{SER}}{\partial \log a_{ij}} \doteq \frac{\text{SER}_{post} - \text{SER}_{pre}}{\text{SER}_{pre}} \frac{1}{p_{ij}} \tag{20}$$

where p_{ij} is the proportional change in the vital rate a_{ij}. Population inertia is not a

linear function of the a_{ij}, thus the elasticities do not sum to unity nor do they quantify the

contribution of the a_{ij} to SER like they do for the geometric population growth rate (de

Kroon et al., 1986). Still, elasticities do provide useful measures of the effect of relative

change in a vital rate on population inertia.

2.4. General Formulas For The 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 changes in initial conditions cause change in population inertia.

Thus, we develop general formulas for this sensitivity as well. To begin, we apply the

quotient rule to differentiate Eq. (10) with respect to a single entry $n_i(0)$ of the initial

population vector:

$$
\begin{aligned}
\frac{\partial \, \text{SER}}{\partial n_i(0)} &= \mathbf{e}^T \mathbf{w}_1 \frac{\partial}{\partial n_i(0)} \left(\frac{\mathbf{v}_1^* \mathbf{n}_0}{\mathbf{e}^T \mathbf{n}_0} \right) \\
&= \mathbf{e}^T \mathbf{w}_1 \left[\frac{\mathbf{e}^T \mathbf{n}_0 \frac{\partial}{\partial n_i(0)} \left(\mathbf{v}_1^* \mathbf{n}_0 \right) - \mathbf{v}_1^* \mathbf{n}_0 \frac{\partial}{\partial n_i(0)} \mathbf{e}^T \mathbf{n}_0}{\left(\mathbf{e}^T \mathbf{n}_0 \right)^2} \right] \\
&= \mathbf{e}^T \mathbf{w}_1 \left[\frac{\mathbf{e}^T \mathbf{n}_0 \left(\overline{v}_i^{(1)} \right) - \mathbf{v}_1^* \mathbf{n}_0}{\left(\mathbf{e}^T \mathbf{n}_0 \right)^2} \right].
\end{aligned}
\tag{21}
$$

We note that the 'initial' point in time can be defined as the point in time from which the

population will be studied forward. We assume for the rest of this section that

$\mathbf{e}^T \mathbf{w}_1 = \|\mathbf{w}_1\| = 1$, $\mathbf{e}^T \mathbf{n}_0 = \|\mathbf{n}_0\| = 1$, and $\mathbf{v}_1$ is real. Then

$$
\frac{\partial \, \text{SER}}{\partial n_i(0)} = v_i^{(1)} - \mathbf{v}_1^T \mathbf{n}_0.
\tag{22}
$$

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

$$
\left. \frac{\partial \, \text{SER}}{\partial n_i(0)} \right|_{\mathbf{w}_1} = v_i^{(1)} - 1.
\tag{23}
$$

Thus, in Eq. (22), knowledge of only the reproductive value and initial population

structure are needed to measure the sensitivity of population inertia 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. 23), then only reproductive value is needed, which is

easily computed from $\mathbf{A}$.

Now we consider perturbations that could affect multiple (st)age classes. To do this, let $\mathbf{u} = [u_1, \cdots, u_n]^T$ 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 $\mathbf{u}$. Then

$$D_{\mathbf{u}}\mathrm{SER} = \nabla\mathrm{SER}^T\mathbf{u}, \tag{24}$$

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

$$\begin{aligned} D_{\mathbf{u}}\mathrm{SER}\big|_{\mathbf{w}_1} &= \nabla\mathrm{SER}^T\mathbf{u} \\ &= (\mathbf{v}_1 - \mathbf{e})^T\mathbf{u}. \end{aligned} \tag{25}$$

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 one perturbs only the ith entry of $\mathbf{w}_1$ (i.e., $\mathbf{u} = [0, \cdots, 0, 1, 0, \cdots, 0]^T$), then the sign of the ith entry of $\mathbf{v}_1 - \mathbf{e}$ dictates the direction that the SER moves away from 1. In this case

$$\left. \frac{\partial\,\text{SER}}{\partial n_i(0)} \right|_{\mathbf{w}_1} = \left. D_{\mathbf{u}}\text{SER} \right|_{\mathbf{w}_1} = v_i^{(1)} - 1. \tag{26}$$

Thus, Eq. (23) is just a special case of the directional derivative (Eq. 25). In addition, if

$\mathbf{u} = \mathbf{w}_1$, then the distribution of individuals among stage classes does not change

following the perturbation ($\mathbf{u}$), so the SER is expected to remain at 1. This is indeed the

case, since $\left. D_{\mathbf{w}_1}\text{SER} \right|_{\mathbf{w}_1} = (\mathbf{v}_1 - \mathbf{e})^{\mathrm{T}} \mathbf{w}_1 = \mathbf{v}_1^{\mathrm{T}} \mathbf{w}_1 - \mathbf{e}^{\mathrm{T}} \mathbf{w}_1 = \mathbf{v}_1^{\mathrm{T}} \mathbf{w}_1 - 1 = 0$.

3. APPLICATIONS AND EXAMPLES

3.1. Age-related Dynamics Of Inertia In An Open Population

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). Furthermore, spatial structuring of

populations can significantly affect population momentum, and more generally,

population inertia (Rogers and Willekens, 1978; Rogers, 1995). In addition to fertility

and survival, dynamics of 'open' populations are affected by immigration and

emigration. Here, we provide a short example illustrating how our formulae can be used

to examine and compare how population inertia is affected by changes in each of the age-

or stage-structured vital rates of an open population.

It is relatively straightforward to incorporate net immigration into projection

models (e.g., Rogers, 1995), but Cooch et al. (2001) present a concise model for

incorporating birth, survival, immigration, and emigration vital rates into a single

projection matrix:

$$\mathbf{A} = \begin{bmatrix} 0 & \cdots & m_x S_0 \eta_0 & \cdots & m_x S_0 \eta_0 \\ S_x \eta_x + I_x & 0 & 0 & \cdots & 0 \\ 0 & \ddots & 0 & \cdots & 0 \\ \vdots & 0 & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & S_x \eta_x + I_x & 0 \end{bmatrix}$$

where $\mathbf{A}$ is constructed in the traditional pre-breeding census format (Caswell, 2001), m_x

is the average number of births per female in age- or stage-class x, S_0 is the probability

of surviving from birth to census in age- or stage-class 1, S_x is the survival probability

from age- or stage-class x to $x + 1$, η_0 and η_x are the corresponding probabilities of

remaining in the population, conditional on being alive (i.e., 1 – emigration probability,

which is called site fidelity), and I_x is the probability that an individual present in the

population at time t in age- or stage-class $x + 1$ was not present in the population at time t

– (census time) in age- or stage-class x (i.e., the probability of immigrating during the

time between censuses from outside the local population). In the example presented here,

we parameterized this model ($\mathbf{A}$) with data based on a female segment of the U.S.

population < 50 years old, counted at 5-year intervals, and growing by 1% per year

(Table 1). Data were based on the 1980, U.S. Southwest life tables presented in Rogers

(1995), but adjusted to fit our example described above. We assumed that the population

initially had a stable population structure and then applied Eqs. (16), (17), and (18) to

calculate the elasticity of population inertia (i.e., the SER) to changes in each of the

aforementioned vital rates.

Of great importance, the sign of the survival, fidelity (η_x), and immigration

elasticities changed from negative to positive with increasing age while the fecundity

elasticity was 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 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). The effect of changing a vital rate on the

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 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 the SER, a more general measure of population

inertia.

Moreover, population inertia affects abundance in the various age classes, which

is known to have profound impacts on the economy (Lee, 2000) and use of natural

resources (Liu et al., 1999, 2003). Thus, our resultant patterns in the elasticity of

population inertia to changes in vital rates across age (see Fig. 2) could be very important

in a variety of situations. From our example, it is quite apparent that change in a given

vital rate for age-class 30 would have a very different effect on population inertia, and

thus abundance, than would the same change in age-class 5 (Fig. 2).

Age-related patterns in population inertia sensitivities and elasticities may be a

general result of significant importance. Although this is just one simple example,

further study of population inertia sensitivities and elasticities across age and stage are as

warranted as the numerous studies of population growth rate sensitivities, elasticities, and selection pressures. Furthermore, population inertia sensitivities and elasticities could prove to be very useful for studying the dynamics of multi-regional populations (Rogers, 1995), and meta-populations (Hanski and Gilpin, 1997) such as source-sink systems (e.g., Koons, 2005).

3.2. Life History And The Sensitivity Of Population Inertia

The study of patterns in population dynamics across populations and species is important because it aids in the understanding of life history evolution (Harvey and Pagel, 1991; Stearns, 1992), and in the development of demographic policy as well as conservation and management of populations (Bos et al., 1994; Fagan et al., 2001). Adding to the repertoire of methods used in comparative demography, our formulas allow one to compare the functional relationship between vital rates and population inertia across populations and across species. Furthermore, the analytical formulae provide a consistent means for comparison that alleviate some pitfalls of numerical simulation.

To provide a brief example of such an application, we used the bird data with stationary growth ($\lambda_1 = 1$) provided in Koons et al. (2006b). Population models were constructed as in Koons et al. (2006b), and we assumed that each population initially had a stable population structure and stationary growth, hence the SER = 1. This served as a nice starting point because any perturbation to these equilibrium conditions produces a SER $\neq$ 1, and it is this 'change' in population inertia that we were interested in comparing across species with different life history attributes. Specifically, we applied Eq. (16) to

the population model (**A**) for each species and calculated the sensitivity of the SER to

changes in fertility, sub-adult survival, and adult survival.

Across the avian life histories, we found that the sensitivity of the SER to changes

in fertility increased with the life history generation time ($p < 0.01$, $R^2 = 0.94$, Fig. 3a) as

did sensitivity of the SER to changes in sub-adult survival ($p < 0.01$, $R^2 = 0.86$, Fig. 3b).

Interestingly, sensitivity of the SER to change in sub-adult survival was negative for

species with a generation time < 10 years but positive for species that mature later in life

and have a longer generation time. Thus, whether changes in sub-adult survival produced

inertia leading to an enlarged or reduced population size relative to an otherwise

equivalent population in its stable population structure depended on the duration of the

sub-adult stage. On the other hand, sensitivity of the SER to change in adult survival

decreased with life history generation time and was always negative (Fig. 3c). Although

statistical support for the latter relationship was weak ($p = 0.12$, $R^2 = 0.27$), this brief

analysis indicates that the functional relationship between vital rates and population

inertia does tend to vary with life history, which is consistent with Koons et al's more in-

depth numerical analysis of population momentum across vertebrate life histories

(2006b). Our equations can be used for analysis following a population's transition to

stationary growth, which would be of interest when studying population momentum, but

can also be used to study non-stationary conditions as well. We suggest use of these new

tools to examine population inertia dynamics in a wide variety of populations and

species.

3.3. Effects Of Initial Population Structure

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 their favor when managing population abundance (MacArthur, 1960; Merrill et al., 2003; Hauser et al., 2006). Plant and animal release and relocation programs 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 specific age or stage classes (Larkin, 1977; Holt and Talbot, 1978). All of these management practices could change population inertia. Thus, we provide an example that illustrates how population inertia is affected by perturbations that add or remove individuals from specific age classes of a population. We use the following matrix **A**, which describes the mean fertility and survival rates of the lesser snow goose (*Chen caerulescens*) population at La Perouse Bay, Manitoba from 1973 to 1990 (Cooch et al., 2001).

$$\mathbf{A} = \begin{bmatrix} 0 & 0.12 & 0.26 & 0.38 & 0.41 \\ 0.83 & 0 & 0 & 0 & 0 \\ 0 & 0.83 & 0 & 0 & 0 \\ 0 & 0 & 0.83 & 0 & 0 \\ 0 & 0 & 0 & 0.83 & 0.83 \end{bmatrix}$$

In **A**, fertilities are represented on the top row and survival probabilities are on the sub-diagonal and bottom-right corner of the matrix. The 1st age class represents young and all others represent adult age classes.

To begin, we calculated the left $\mathbf{v}_1 = \begin{bmatrix} 0.34 & 0.44 & 0.52 & 0.56 & 0.57 \end{bmatrix}^{\mathrm{T}}$ and right

$\mathbf{w}_1 = \begin{bmatrix} 0.46 & 0.36 & 0.28 & 0.21 & 0.73 \end{bmatrix}^{\mathrm{T}}$ eigenvectors of $\mathbf{A}$. To simplify our scenario, we

assumed that population structure was initially stable (i.e., $\mathbf{n}_0 = \mathbf{w}_1$), indicating SER

initially $= 1$. We also normalized $\mathbf{w}_1$ into a unit vector (i.e., $\|\mathbf{w}_{1,nor.}\| = 1$), and

normalized $\mathbf{v}_1$, such that $\mathbf{v}_{1,nor.} = \mathbf{v}_1 \|\mathbf{w}_1\|$, which allowed us to use Eqs. (25) and (26) to

easily address our scenario. In addition, the normalized right and left eigenvectors are

still eigenvectors of $\mathbf{A}$, and the condition $\mathbf{v}_i^* \mathbf{w}_i = 1$ is maintained. Rounded to the second

decimal, $\mathbf{w}_{1,nor.} = \begin{bmatrix} 0.23 & 0.17 & 0.14 & 0.10 & 0.36 \end{bmatrix}^{\mathrm{T}}$ and

$\mathbf{v}_{1,nor.} = \begin{bmatrix} 0.70 & 0.90 & 1.06 & 1.15 & 1.17 \end{bmatrix}^{\mathrm{T}}$.

Next, we used the directional derivative to measure the sensitivity of population

inertia to a variety of perturbations to initial population structure (Table 2). It is readily

seen that 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 ∇SER or $v_i^{(1)}$ -1. For

example, a unit increase in the 1st age class decreases population inertia (SER < 1), a unit

increase in an older adult age class increases population inertia (SER > 1), and unit

decreases produce opposite results (Table 2). Furthermore, perturbations to multiple age

classes produce intermediate, but perhaps more realistic results. Perturbations equal to

the stable age distribution ($\mathbf{w}_{1,nor.}$) do not change population inertia at all (SER still $= 1$;

Table 2).

Compared to the stable age distribution of $\mathbf{A}$, removing young (e.g., through

clutch removal), releasing adults, or both, would allow a goose manager to quickly

increase population inertia because each action shifts age structure towards reproducing adults. On the other hand, releasing young, removing adults (via harvest or live trapping), or both, would allow the manager to quickly decrease population inertia because these practices shift age structure towards young. However, it is important to remember that these results pertain only to the effects of directly changing population structure, not the effects of perturbing vital rates, which are presented above.

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 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 (see Koons, 2005). Similarly, invasion of non-native plants and animals can lead to substantial economic and environmental damage. Management aimed towards minimizing the SER would be of interest in the management of invasive species (Keyfitz and Caswell, 2005; Koons et al., 2006a) and our formulae could help refine management agendas in these situations. (Matlab code for example calculations can be attained by e-mailing DNK.)

4. CLOSING REMARKS

Population inertia is a measure related to population size rather than growth rate, and unlike the growth rate, population size is very responsive to initial population structure (Tuljapurkar and Lee, 1997). Direct or indirect 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. Sensitivities have been developed for population size (Fox and Gurevitch, 2000;

Yearsley, 2004). However, we have drawn upon theory developed by Caswell (1980) to derive a suite of sensitivity formulae for the SER that explicitly show that population inertia depends on both reproductive value and population structure (Tuljapurkar and Lee, 1997; Eq. 13). These formulae differ from those for population size itself because the SER is a ratio measuring the inertial effect 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 refer to asymptotic measures of population dynamics (e.g., r, λ_1, T) making the SER especially useful because it provides a direct comparison of the dynamics resulting from changes in the vital rates and population structure to the stable population dynamics (Fig. 1b). Thus, the 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, population biology, evolution, conservation, and natural resource management as well as many other arenas.

Formulas relating change in underlying vital rates to change in the asymptotic population growth rate (e.g., Caswell 1978), transient dynamics (Fox and Gurevitch, 2000; Caswell, 2001; Yearsley, 2004; Koons et al. 2005), and inertia in long-term population size (here) are all needed to better understand population dynamics from evolutionary and applied points of view. We encourage further exploration of the behavior of population inertia in nature, as well as theoretical work on the maximization, minimization, and control of population inertia (e.g., Koons, 2005; Hauser et al., 2006).

ACKNOWLEDGMENTS

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Appendix 1.

Here, we establish Eq. (7), namely,

$$M_{\mathbf{r}_0} = \frac{\left|\mathbf{v}_h^* \, \mathbf{n}_0\right| \left\|\mathbf{r}_0\right\|}{\left|\mathbf{v}_h^* \, \mathbf{r}_0\right| \left\|\mathbf{n}_0\right\|},$$

under the assumption $\left|\lambda_i\right| < \left|\lambda_h\right|$ for $i > h$, where h is the lesser of the height of $\mathbf{n}_0$ and

the height of $\mathbf{r}_0$. We can write $\mathbf{n}_0 = \sum_{i=h}^{n} c_i \mathbf{w}_i$ and $\mathbf{r}_0 = \sum_{i=h}^{n} d_i \mathbf{w}_i$ with either $c_h \neq 0$ or

$d_h \neq 0$. We have, using Eq. (2),

$$M_{\mathbf{r}_0} \frac{\left\|\mathbf{n}_0\right\|}{\left\|\mathbf{r}_0\right\|} = \lim_{t \to \infty} \frac{\left\|\mathbf{n}_t\right\|}{\left\|\mathbf{r}_t\right\|} = \lim_{t \to \infty} \frac{\left\|\sum_{i=h}^{n} c_i \lambda_i^t \mathbf{w}_i\right\|}{\left\|\sum_{i=h}^{n} d_i \lambda_i^t \mathbf{w}_i\right\|} = \lim_{t \to \infty} \frac{\left\|\sum_{i=h}^{n} c_i \left(\lambda_i / \lambda_h\right)^t \mathbf{w}_i\right\|}{\left\|\sum_{i=h}^{n} d_i \left(\lambda_i / \lambda_h\right)^t \mathbf{w}_i\right\|}$$

$$= \frac{\left\|c_h \mathbf{w}_h\right\|}{\left\|d_h \mathbf{w}_h\right\|} = \frac{\left|c_h\right|}{\left|d_h\right|} = \frac{\left|\mathbf{v}_h^* \, \mathbf{n}_0\right|}{\left|\mathbf{v}_h^* \, \mathbf{r}_0\right|},$$

and the equality follows. For the fourth equality, we have used the fact that for $i > h$,

$\left|\lambda_i\right| < \left|\lambda_h\right|$, implying $\lim_{t \to \infty} \left(\lambda_i / \lambda_h\right)^t = 0$. Note also that if $d_h = 0$, then $c_h \neq 0$, so the

limit is ∞. In this case, $\mathbf{v}_h^* \mathbf{r}_0 = 0$, so the final fraction is interpreted as being ∞ in

accordance with our stated convention.

Appendix 2.

We discuss in detail some technical issues regarding our derivation of the population inertia sensitivity formula presented in Eq. (16) of the text. To begin, fix a pair (i, j) and view the matrix $\mathbf{A}$ as a function of $t = a_{ij}$ alone (this dependence is indicated by writing $\mathbf{A} = \mathbf{A}(t)$). Let I be an open interval of real numbers such that $\mathbf{A}(t)$ is irreducible for all $t \in I$ and fix $t_0 \in I$. We claim that the dominant right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors of $\mathbf{A}$ can be chosen in such a way that

(A1) $\mathbf{w}_1$ and $\mathbf{v}_1$ are both differentiable functions of t on the interval I,

(A2) $\langle \mathbf{w}_1(t_0), \mathbf{w}_1(t_0) \rangle = 1$,

(A3) $\langle \mathbf{w}_1', \mathbf{v}_1 \rangle = 0$ and $\langle \mathbf{w}_1, \mathbf{v}_1' \rangle = 0$,

(A4) $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle = 1$.

Here, the prime symbol (') denotes derivative with respect to t and the equations in A3 and A4 are understood to be identities, that is, valid for all $t \in I$. Also, for vectors $\mathbf{v}$ and $\mathbf{w}$ we are writing, for clarity, $\langle \mathbf{v}, \mathbf{w} \rangle$ instead of $\mathbf{v}^* \mathbf{w}$. (Reasons for choosing the eigenvectors to satisfy A1-A4 are given in the remarks below.)

We first establish a general result.

Lemma: Let $\mathbf{x}$ and $\mathbf{y}$ be n-dimensional real vector functions on an open real interval I. Assume that $\mathbf{x}$ is differentiable, $\mathbf{x}'$ and $\mathbf{y}$ are continuous, and $\langle \mathbf{x}(t), \mathbf{y}(t) \rangle \neq 0$ for all $t \in I$. Let c_0 and t_0 be real numbers with $t_0 \in I$ and $c_0 > 0$. There exists a differentiable positive real-valued function c on I such that $\langle (c\mathbf{x})', \mathbf{y} \rangle = 0$ and $c(t_0) = c_0$.

Proof: We have $\langle (c\mathbf{x})', \mathbf{y} \rangle = c' \langle \mathbf{x}, \mathbf{y} \rangle + c \langle \mathbf{x}', \mathbf{y} \rangle$, so the desired function c is a solution to

the initial value problem $c' + pc = 0$, $c(t_0) = c_0$, where $p = \langle \mathbf{x}', \mathbf{y} \rangle / \langle \mathbf{x}, \mathbf{y} \rangle$. This has a

unique solution, namely $c(t) = c_0 \exp\left(-\int_{t_0}^{t} p(u)\, du \right)$, which is evidently positive.

For $t \in I$, let $\hat{\mathbf{w}}_1(t)$ and $\hat{\mathbf{v}}_1(t)$ denote the unique positive right and left

eigenvectors of $\mathbf{A}(t)$ corresponding to $\lambda_1(t)$ such that $\langle \hat{\mathbf{w}}_1(t), \hat{\mathbf{w}}_1(t) \rangle = 1$ and

$\langle \hat{\mathbf{v}}_1(t), \hat{\mathbf{v}}_1(t) \rangle = 1$. This is guaranteed by our assumption that $\mathbf{A}(t)$ is irreducible for all

$t \in I$. Then $\hat{\mathbf{w}}_1$ and $\hat{\mathbf{v}}_1$ are continuously differentiable vector functions on I.

Fix $t_0 \in I$. Apply the lemma with $\mathbf{x} = \hat{\mathbf{w}}_1, \mathbf{y} = \hat{\mathbf{v}}_1, c_0 = 1$. Then $\mathbf{w}_1 = c\hat{\mathbf{w}}_1$, with c

as in the lemma, is a differentiable vector function satisfying $\langle \mathbf{w}_1', \hat{\mathbf{v}}_1 \rangle = 0$ and

$\mathbf{w}_1(t_0) = \hat{\mathbf{w}}_1(t_0)$. Apply the lemma again, but this time with $\mathbf{x} = \hat{\mathbf{v}}_1, \mathbf{y} = \mathbf{w}_1$,

$c_0 = \langle \hat{\mathbf{w}}_1(t_0), \hat{\mathbf{v}}_1(t_0) \rangle^{-1}$. Then $\mathbf{v}_1 = c\hat{\mathbf{v}}_1$, with c as in the lemma, is a differentiable vector

function satisfying $\langle \mathbf{v}_1', \mathbf{w}_1 \rangle = 0$ and $\mathbf{v}_1(t_0) = \langle \hat{\mathbf{w}}_1(t_0), \hat{\mathbf{v}}_1(t_0) \rangle^{-1} \hat{\mathbf{v}}_1(t_0)$. Note that

$\langle \mathbf{w}_1', \mathbf{v}_1 \rangle = \langle \mathbf{w}_1', c\hat{\mathbf{v}}_1 \rangle = c \langle \mathbf{w}_1', \hat{\mathbf{v}}_1 \rangle = 0$. Now $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle' = \langle \mathbf{w}_1', \mathbf{v}_1 \rangle + \langle \mathbf{w}_1, \mathbf{v}_1' \rangle = 0$, so $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle$

does not depend on t. Since $\langle \mathbf{w}_1(t_0), \mathbf{v}_1(t_0) \rangle = \langle \hat{\mathbf{w}}_1(t_0), \langle \hat{\mathbf{w}}_1(t_0), \hat{\mathbf{v}}_1(t_0) \rangle^{-1} \hat{\mathbf{v}}_1(t_0) \rangle = 1$, it

follows that $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle = 1$ on I. This establishes the claim that $\mathbf{w}_1$ and $\mathbf{v}_1$ can be chosen

to satisfy A1-A4.

Remarks: In view of A1 and A4, we can use $\mathbf{w}_1$ and $\mathbf{v}_1$ in Eq. (9) to view the SER as a

differentiable function of t on the interval I. Writing the differential $d\mathbf{w}_1 = \mathbf{w}_1' dt$ in the

form $d\mathbf{w}_1 = \sum_{m=1}^{s} a_m \mathbf{w}_m$ as in Caswell (2001:249) and taking the inner product with $\mathbf{v}_1$ of both sides, we see that $a_1 = 0$ since $\left\langle \mathbf{w}_1', \mathbf{v}_1 \right\rangle = 0$ (by A3). Therefore, the derivation Caswell gives of the right eigenvector sensitivity formula (Eq. 14 in our paper) is valid for this choice of $\mathbf{w}_1$ and $\mathbf{v}_1$ (with the remaining eigenvectors chosen arbitrarily). Since $\left\langle \mathbf{w}_1, \mathbf{v}_1' \right\rangle = 0$ (by A3), the left eigenvector sensitivity formula (Eq. 15) is valid as well.

Finally, we point out that if a computer program automatically scales the eigenvectors so that $\left\langle \mathbf{w}_1, \mathbf{w}_1 \right\rangle = 1$ and $\left\langle \mathbf{w}_1, \mathbf{v}_1 \right\rangle = 1$ (as does Matlab), then, in view of A2 and A4, it gives the desired results when applied to our SER sensitivity formula in Eq. (16) at any fixed parameter value $a_{ij} = t_0 \in I$.

Table 1. Values of survival probability (S), local population fidelity (η, not to be confused with fidelity towards a mate), immigration probability (I) and fecundity (m, female births per female between and including age x and $x + 4$) for the female segment of the U.S. Southwest population < 50 years old, counted at 5-year intervals, and growing by 1 % per year.

| Age x | Vital Rates[a] | | | |
	S	η	I	m
0	0.938	0.956	-	0
5	0.971	0.973	0.087	0.0008
10	0.977	0.979	0.076	0.0978
15	0.968	0.974	0.102	0.2880
20	0.956	0.963	0.144	0.3698
25	0.955	0.962	0.144	0.2760
30	0.962	0.970	0.104	0.1313
35	0.969	0.978	0.065	0.0389
40	0.970	0.985	0.042	0.0067
45	0.966	0.988	0.030	0.0004

a – Data were based on life tables presented in Rogers (1995), but adjusted to fit our example described in the text.

Table 2. The sensitivity of population inertia to unit changes $\mathbf{u}$ in the initial population structure of the lesser snow goose population at La Perouse Bay, Manitoba, indicated by the directional derivative $D_{\mathbf{u}}\text{SER}\big|_{\mathbf{w}_1}$, and the effect of the perturbation on the SER. We used the normalized left eigenvector $\mathbf{v}_{1,nor.} = \begin{bmatrix} 0.70 & 0.90 & 1.06 & 1.15 & 1.17 \end{bmatrix}^T$, and the following gradient of the SER: $\nabla\text{SER} = \begin{bmatrix} -0.30 & -0.10 & 0.06 & 0.15 & 0.17 \end{bmatrix}^T$, each rounded to the second decimal.

$\mathbf{u}$[a]	$D_{\mathbf{u}}\text{SER}\big|_{\mathbf{w}_1}$	Value of SER after perturbation
$[1\ 0\ 0\ 0\ 0]^T$	-0.30	< 1
$[0\ 0\ 1\ 0\ 0]^T$	0.06	> 1
$[0\ 0\ 0\ 0\ 1]^T$	0.17	> 1
$[-1\ 0\ 0\ 0\ 0]^T$	0.30	> 1
$[0\ 0\ -1\ 0\ 0]^T$	-0.06	< 1
$[0\ 0\ 0\ 0\ -1]^T$	-0.17	< 1
$[0.2\ 0.2\ 0.2\ 0.2\ 0.2]^T$	-0.003	< 1
$[-0.2\ -0.2\ -0.2\ -0.2\ -0.2]^T$	0.003	> 1
$[0.23\ 0.17\ 0.14\ 0.10\ 0.36]^T$ [b]	0	1

a – Rounded to the second decimal

b – The stable age distribution

Figure 1. Graphical examples of a) Keyfitz's "population momentum" showing increased population size caused by an unstable population structure (solid line) relative to the size of an otherwise equivalent population growing according to its stable population structure and a stationary growth rate (dashed line), and b) "population inertia", which is essentially the same phenomenon, but not restricted in definition to populations that eventually attain the stationary population growth rate (e.g., a growing population is shown here). Measures of population inertia are given in section 2.2.

Figure 2. The 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 (section 3.1).

Figure 3. The relationship between life history generation time and the sensitivity of the Stable Equivalent Ratio (SER) to changes in a) fertility, b) sub-adult survival, and c) adult survival for initially stationary populations of selected avian species. The scale of the y-axes differs among graphs a, b, and c. (Life history data comes from Koons et al. 2006b).

a)

b)