

David N. Koons, Randall R. Holmes, and James B. Grand. 2007. Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology* 88:2857–2867.

Appendix B. Proof of Eq. 13 and that the SER elasticities associated with the matrix entries a_{ij} sum to zero.

Proof of Eq. 13

We discuss in detail some technical issues regarding our derivation of the SER sensitivity formula presented in Eq. 13 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

(B.1) \mathbf{w}_1 and \mathbf{v}_1 are both differentiable functions of t on the interval I ,

(B.2) $\langle \mathbf{w}_1(t_0), \mathbf{w}_1(t_0) \rangle = 1$,

(B.3) $\langle \mathbf{w}_1', \mathbf{v}_1 \rangle = 0$ and $\langle \mathbf{w}_1, \mathbf{v}_1' \rangle = 0$,

(B.4) $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle = 1$.

Here, the prime symbol (') denotes derivative with respect to t and Eqs. B.3 and B.4 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 Eqs. B.1 to B.4 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 Eqs. B.1 to B.4.

Remarks: In view of Eqs. B.1 and B.4, we can use \mathbf{w}_1 and \mathbf{v}_1 in Eq. 8 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 $\langle \mathbf{w}'_1, \mathbf{v}_1 \rangle = 0$ (by Eq. B.3). Therefore, the derivation Caswell gives of the right eigenvector sensitivity formula (Eq. 11 in our paper) is valid for this choice of \mathbf{w}_1 and \mathbf{v}_1 (with the remaining eigenvectors chosen arbitrarily). Since $\langle \mathbf{w}_1, \mathbf{v}'_1 \rangle = 0$ (by Eq. B.3), the left eigenvector sensitivity formula (Eq. 12) is valid as well. Finally, we point out that if a computer program automatically scales the eigenvectors so that $\langle \mathbf{w}_1, \mathbf{w}_1 \rangle = 1$ and $\langle \mathbf{w}_1, \mathbf{v}_1 \rangle = 1$ (as does Matlab), then, in view of Eqs. B.2 and B.4, it gives the desired results when applied to our SER sensitivity formula in Eq. 13 at any fixed parameter value $a_{ij} = t_0 \in I$.

Proof that the SER elasticities associated with the a_{ij} sum to zero

We claim that the elasticities of SER relative to the various matrix entries a_{ij} , $1 \leq i, j \leq n$, all sum to zero (see Eq. 16 in the text). In symbols,

$$\sum_{i,j} \frac{a_{ij}}{\text{SER}} \frac{\partial \text{SER}}{\partial a_{ij}} = 0. \quad (\text{B.5})$$

In order to prove this, we begin with some observations. First, $\sum_j a_{ij} w_j^{(1)}$ is the i th entry of $\mathbf{A}\mathbf{w}_1 = \lambda_1 \mathbf{w}_1$ and is thus equal to $\lambda_1 w_i^{(1)}$. Also, $\sum_i w_i^{(1)} \bar{v}_i^{(m)} = \mathbf{v}_m^* \mathbf{w}_1$, which is 0 if $m \neq 1$. Therefore, using Eq. 11 in the text we get

$$\sum_{i,j} a_{ij} \frac{\partial \mathbf{w}_1}{\partial a_{ij}} = \sum_{i,j} a_{ij} w_j^{(1)} \sum_{m \neq 1} \frac{\bar{v}_i^{(m)}}{\lambda_1 - \lambda_m} \mathbf{w}_m = \sum_{m \neq 1} \frac{\lambda_1}{\lambda_1 - \lambda_m} \left(\sum_i w_i^{(1)} \bar{v}_i^{(m)} \right) \mathbf{w}_m = 0. \quad (\text{B.6})$$

Similarly, using Eq. 12 we get

$$\sum_{i,j} a_{ij} \frac{\partial \mathbf{v}_1^*}{\partial a_{ij}} = 0. \quad (\text{B.7})$$

Now our claim follows from Eq. 10 in the text:

$$\sum_{i,j} \frac{a_{ij}}{\text{SER}} \frac{\partial \text{SER}}{\partial a_{ij}} = \frac{1}{\text{SER}} \frac{1}{\mathbf{e}^T \mathbf{n}_0} \mathbf{e}^T \left[\left(\mathbf{v}_1^* \mathbf{n}_0 \right) \left(\sum_{i,j} a_{ij} \frac{\partial \mathbf{w}_1}{\partial a_{ij}} \right) + \left(\left(\sum_{i,j} a_{ij} \frac{\partial \mathbf{v}_1^*}{\partial a_{ij}} \right) \mathbf{n}_0 \right) \mathbf{w}_1 \right] = 0. \quad (\text{B.8})$$

We thank an anonymous reviewer for suggesting this property of SER elasticities.

[\[Back to E088-177\]](#)