Appendices

A  First derivatives of $S = \frac{d \text{vec} A}{d \theta^\top}$ and $T = \frac{d \lambda}{d \text{vec}^\top A}$

In (30), we defined

$$S = \frac{d \text{vec} A}{d \theta^\top} \quad \text{and} \quad T = \frac{d \lambda}{d \text{vec}^\top A} = w^\top \otimes v^\top.$$  \hfill (A-1)

To evaluate (34), we require the first derivatives of $S$ and $T$. For the first derivative of $S$:

$$\frac{d \text{vec} S}{d \theta^\top} = \frac{d}{d \theta^\top} \text{vec} \left[ \frac{d \text{vec} A}{d \theta^\top} \right].$$  \hfill (A-2)

Apply the commutation matrix (vec-permutation matrix) $K_{m,n}$, a constant matrix of 0’s and 1’s that can be calculated using the MATLAB function provided in Appendix D. For any $m \times n$ matrix $A$, there is a unique $mn \times mn$ matrix $K_{m,n}$ such that:

$$K_{m,n} \text{vec} A = \text{vec}(A^\top).$$  \hfill (A-3)

Using both the commutation matrix and the definition of the Hessian matrix in (9):

$$\frac{d \text{vec} S}{d \theta^\top} = \frac{d}{d \theta^\top} \text{vec} \left[ \frac{d \text{vec} A}{d \theta^\top} \right] = \frac{d}{d \theta^\top} K_{s,n^2} \text{vec} \left[ \left( \frac{d \text{vec} A}{d \theta^\top} \right)^\top \right] = K_{s,n^2} H \left[ \text{vec} A; \theta \right].$$  \hfill (A-4)

Note that for a $m \times n$ matrix $X$ and a $p \times q$ matrix $Y$,

$$K_{p,m} (X \otimes Y) = (Y \otimes X) K_{q,n}.$$  \hfill (A-7)
\[ K_{n,1} = K_{1,n} = I_n \]  

(A-8)  

so (35) becomes

\[
(I_s \otimes T) \frac{d \text{vec } S}{d \theta^\top} = (I_s \otimes T) K_{s,n} H \left[ \text{vec } A; \theta \right] 
= (T \otimes I_s) H \left[ \text{vec } A; \theta \right].
\]  

(A-9)  

(A-10)  

To find (36), differentiate the expression for \( T \)

\[
\frac{d \text{vec } T}{d \theta^\top} = \frac{d}{d \theta^\top} \text{vec} \left[ \frac{d \lambda}{d \text{vec } A^\top} \right]
\]  

(A-11)  

and use the chain rule to rewrite it in terms of the derivative with respect to \( A \)

\[
\frac{d \text{vec } T}{d \theta^\top} = \frac{d}{d \text{vec } A^\top} \text{vec} \left[ \frac{d \lambda}{d \text{vec } A^\top} \right] \frac{d \text{vec } A}{d \theta^\top}.
\]  

(A-12)  

The first part of (A-12) is equivalent to the Hessian expression (9), so:

\[
\frac{d \text{vec } T}{d \theta^\top} = H \left[ \lambda; \text{vec } A \right] S.
\]  

(A-13)  

B  

Second derivatives of \( R_0 \) to lower-level parameters: \( H \left[ R_0; \theta \right] \)

In Section 3.3, we calculated the second derivatives of the net reproductive rate \( R_0 \) with respect to \( U \) and \( F \). Here, we present the fully general second derivatives of \( R_0 \) with respect to a parameter vector \( \theta \).

As written in (47), the general expression for the Hessian of \( R_0 \) with respect to \( \theta \) is

\[
H \left[ R_0; \theta \right] = \frac{1}{2} (B + B^\top)
\]  

(B-1a)
where
\[
B = (w_R^T \otimes v_R^T \otimes I_s)H [\text{vec}R; \theta] + \left( \frac{d\text{vec}R}{d\theta^T} \right)^T H [R_0; \text{vec}R] \frac{d\text{vec}R}{d\theta^T} \quad (\text{B-1b})
\]
and \(w_R\) and \(v_R\) are the right and left eigenvectors of \(R\). As noted in the main text, evaluating \(B\) requires the second derivatives of \(R_0\) with respect to \(R\) (the Hessian \(H [R_0; \text{vec}R]\), which is given by (25) using the dominant eigenvalues and eigenvectors of \(R\) rather than those of \(A\), and the first and second derivatives of \(R\) with respect to \(\theta\). We will now calculate these derivatives of \(R\) with respect to \(\theta\).

The first derivatives of \(R\) with respect to \(\theta\) are
\[
\frac{d\text{vec}R}{d\theta^T} = (N^T \otimes I_n) \frac{d\text{vec}F}{d\theta^T} + (N^T \otimes R) \frac{d\text{vec}U}{d\theta^T} . \quad (\text{B-2})
\]

The second derivatives of \(R\) with respect to \(\theta\) are given by the definition of the Hessian matrix (9):
\[
H [\text{vec}R; \theta] = \frac{d}{d\theta^T} \text{vec} \left[ \left( \frac{d\text{vec}R}{d\theta^T} \right)^T \right] \quad (\text{B-3})
\]
\[
= \frac{d}{d\theta^T} \text{vec} \left[ \left( \frac{d\text{vec}F}{d\theta^T} \right)^T (N \otimes I_n) + \left( \frac{d\text{vec}U}{d\theta^T} \right)^T (N \otimes R^T) \right] . \quad (\text{B-4})
\]

To evaluate this expression, we will use the following rule (Magnus 2010) for derivatives of matrix products: given matrices \(Y (n \times v)\) and \(X (m \times n)\), the derivative of their product with respect to a third matrix \(Z (p \times q)\) is
\[
\frac{d\text{vec}(XY)}{d(\text{vec}Z)^T} = (Y^T \otimes I_m) \frac{d\text{vec}X}{d(\text{vec}Z)^T} + (I_v \otimes X) \frac{d\text{vec}Y}{d(\text{vec}Z)^T} . \quad (\text{B-5})
\]
Applying this product rule for matrix derivatives to (B-4) gives

\[
H [\text{vec}\, R; \theta] = \left( (N \otimes I_n)^\top \otimes I_s \right) \frac{d}{d\theta^\top} \text{vec} \left[ \left( \frac{d\text{vec} F}{d\theta^\top} \right)^\top \right] + \left( I_n^2 \otimes \left( \frac{d\text{vec} F}{d\theta^\top} \right)^\top \right) \frac{d}{d\theta^\top} \text{vec} (N \otimes I_n)
\]

\[
+ \left( (N \otimes R^\top)^\top \otimes I_s \right) \frac{d}{d\theta^\top} \text{vec} \left[ \left( \frac{d\text{vec} U}{d\theta^\top} \right)^\top \right] + \left( I_n^2 \otimes \left( \frac{d\text{vec} U}{d\theta^\top} \right)^\top \right) \frac{d}{d\theta^\top} \text{vec} (N \otimes R^\top)
\]

(B-6)

and recognizing Hessian matrices of the form (9), we obtain

\[
H [\text{vec}\, R; \theta] = (N^\top \otimes I_{ns}) H [\text{vec}\, F; \theta] + \left( I_n^2 \otimes \left( \frac{d\text{vec} F}{d\theta^\top} \right)^\top \right) \frac{d}{d\theta^\top} \text{vec} (N \otimes I_n)
\]

\[
+ (N^\top \otimes R \otimes I_s) H [\text{vec}\, U; \theta] + \left( I_n \otimes \left( \frac{d\text{vec} U}{d\theta^\top} \right)^\top \right) \frac{d}{d\theta^\top} \text{vec} (N \otimes R^\top).
\]

(B-7)

Applying (51), the derivatives of Kronecker products appearing in (B-7) are

\[
\frac{d}{d\theta^\top} \text{vec} (N \otimes I_n) = (I_n \otimes K_{n,n} \otimes I_n) \left( I_n^2 \otimes \text{vec} [I_n] \right) \frac{d\text{vec} N}{d\theta^\top}
\]

(B-8)

\[
\frac{d}{d\theta^\top} \text{vec} (N \otimes R^\top) = (I_n \otimes K_{n,n} \otimes I_n) \left( I_n^2 \otimes \text{vec} [R^\top] \right) \frac{d\text{vec} N}{d\theta^\top} + (\text{vec} N \otimes I_{n^2}) \frac{d\text{vec} R^\top}{d\theta^\top}
\]

(B-9)

and note that

\[
\frac{d\text{vec} N}{d\theta^\top} = (N^\top \otimes N) \frac{d\text{vec} U}{d\theta^\top}
\]

(B-10)

\[
\frac{d\text{vec} R^\top}{d\theta^\top} = K_{n,n} \frac{d\text{vec} R}{d\theta^\top}
\]

(B-11)

where \( \frac{d\text{vec} R}{d\theta^\top} \) is given by (B-2). Substitute (B-10) and (B-11) into (B-8) and (B-9), then back into (B-7) to obtain \( H [\text{vec}\, R; \theta] \).

While the expression for \( H [\text{vec}\, R; \theta] \) may appear complicated, note that it simplifies considerably if only one of \( U \) or \( F \) is a function of \( \theta \), so that either \( \frac{d\text{vec} F}{d\theta^\top} \) or \( \frac{d\text{vec} U}{d\theta^\top} \) is a matrix of zeros (i.e., the parameters of interest affect only fertility or transitions, but not both).
If only $U$ depends on $\theta$:

$$H[\text{vec}R; \theta] = (N^T \otimes R \otimes I_n) H[\text{vec}U; \theta] + \left[I_{n^2} \otimes \left(\frac{d\text{vec}U}{d\theta^T}\right)^T\right] \frac{d}{d\theta^T} \text{vec}(N \otimes R^T).$$ \hspace{1cm} (B-12)

If only $F$ depends on $\theta$:

$$H[\text{vec}R; \theta] = (N^T \otimes I_{ns}) H[\text{vec}F; \theta].$$ \hspace{1cm} (B-13)

Ultimately, substitute $H[\text{vec}R; \theta]$ as given by (B-7) (or B-12 and B-13 if appropriate), and \(\frac{d\text{vec}R}{d\theta^T}\) as given by (B-2), back into (B-1) to obtain $H[R_0; \theta]$.

**B.1 Life cycles with only one type of offspring**

In the common case where there is only one type of offspring (stage 1), the expression for $H[R_0; \theta]$ simplifies considerably. In this case, the fertility matrix $F$ has nonzero entries only in its first row, and $R = FN$ is an upper triangular matrix. Then $R_0$, the dominant eigenvalue of $R$, is the $(1,1)$ entry of $R$:

$$R_0 = e_1^T(R)e_1$$ \hspace{1cm} (B-14)

where $e_1$ is the $n \times 1$ vector with 1 as its first entry and zeros elsewhere (Caswell 2009).

The first differential of $R_0$ is then

$$dR_0 = e_1^T(dR)e_1$$ \hspace{1cm} (B-15)

$$= (e_1^T \otimes e_1^T) d\text{vec}R.$$ \hspace{1cm} (B-16)

By the first identification theorem (10),

$$\frac{dR_0}{d\theta^T} = (e_1^T \otimes e_1^T) \frac{d\text{vec}R}{d\theta^T}$$ \hspace{1cm} (B-17)
and by the definition of the Hessian matrix (9):

\[
H[R_0; \theta] = \frac{d}{d\theta} \text{vec} \left[ \left( \frac{dR_0}{d\theta^T} \right)^T \right] = \frac{d}{d\theta} \text{vec} \left[ \left( \frac{d\text{vec}R}{d\theta^T} \right)^T (e_1 \otimes e_1) \right].
\] (B-18)

Applying the product rule for matrix derivatives in (B-5) to (B-19),

\[
H[R_0; \theta] = (e_1^T \otimes e_1^T \otimes I_s) \frac{d}{d\theta} \text{vec} \left[ \left( \frac{d\text{vec}R}{d\theta^T} \right)^T \right] = (e_1^T \otimes e_1^T \otimes I_s) H[\text{vec}R; \theta]
\] (B-20)

where \( H[\text{vec}R; \theta] \) is given by (B-7) (or B-12 and B-13 if appropriate).

C Sensitivity of the stochastic growth rate

As shown in Caswell (2001), Tuljapurkar’s (1982) approximation for the stochastic growth rate can be written as

\[
\log \lambda_s \approx \log \lambda - \frac{DCD^T}{2\lambda^2}
\] (C-1)

where \( \mathbf{C} \) is the symmetric covariance matrix for the population projection matrix and \( \mathbf{D} \) is the Jacobian matrix (in this case, a row vector) for the dominant eigenvalue \( \lambda \) of the mean population matrix \( \bar{A} \):

\[
\mathbf{D} = D[\lambda; \text{vec} \bar{A}] = \frac{\partial \lambda}{\partial \text{vec}^T \bar{A}}.
\] (C-2)

To find the sensitivity of the stochastic growth rate to \( \bar{A} \), differentiate (C-1) with respect to
\[ \frac{\partial \log \lambda_s}{\partial \text{vec}^\top \bar{A}} = \frac{D}{\lambda} + \frac{D}{\lambda^3} (\text{DCD}^\top) - \frac{1}{2\lambda^2} \frac{\partial (\text{DCD}^\top)}{\partial \text{vec}^\top A} \]  
\[ = \frac{D}{\lambda} \left( 1 + \frac{\text{DCD}^\top}{\lambda^2} \right) - \frac{1}{2\lambda^2} \frac{\partial (\text{DCD}^\top)}{\partial \text{vec}^\top A} . \]  

To evaluate the derivative of $\text{DCD}^\top$ with respect to $\bar{A}$ in the second term, we will apply the product rule for vector derivatives (Magnus 2010). Given vectors $y$ ($n \times 1$) and $x$ ($1 \times n$), the derivative of their product with respect to a third vector $z$ is

\[ \frac{d\text{vec}(xy)}{d\text{vec}^\top z} = y^\top \frac{d\text{vec}x}{d\text{vec}^\top z} + x \frac{d\text{vec}y}{d\text{vec}^\top z} . \]  

Because $\text{DCD}^\top$ is a scalar, $\text{vec}(\text{DCD}^\top) = \text{DCD}^\top$. Thus

\[ \frac{\partial (\text{DCD}^\top)}{\partial \text{vec}^\top A} = \text{DC}^\top \frac{\partial \text{vec}D}{\partial \text{vec}^\top A} + \text{DC} \frac{\partial \text{vec}(D^\top)}{\partial \text{vec}^\top A} . \]  

Note that the Hessian of $\lambda$ with respect to $\bar{A}$ is

\[ H \left[ \lambda; \text{vec} \bar{A} \right] = \frac{d}{d\text{vec}^\top A} \text{vec} \left[ \left( \frac{d\lambda}{d\text{vec}^\top A} \right)^\top \right] \]  
\[ = \frac{\partial \text{vec}(D^\top)}{\partial \text{vec}^\top A} = \frac{\partial \text{vec}(D)}{\partial \text{vec}^\top A} . \]  

Letting $H = H \left[ \lambda; \text{vec} \bar{A} \right]$ and noting that $C$ is a symmetric matrix, (C-6) simplifies to

\[ \frac{\partial (\text{DCD}^\top)}{\partial \text{vec}^\top A} = \text{DC}^\top H + DCH \]  
\[ = 2DCH . \]  

Substituting (C-10) into (C-4), we see that the sensitivity of the stochastic growth rate with
respect to $A$ is

$$\frac{\partial \log \lambda_s}{\partial \text{vec}^\top A} = \frac{D}{\lambda} \left( 1 + \frac{\text{DCD}^\top}{\lambda^2} \right) - \frac{\text{DCH}}{\lambda^2} \quad (C-11)$$

$$= \frac{D}{\lambda} \left( 1 - \frac{\text{CH}}{\lambda} + \frac{\text{DCD}^\top}{\lambda^2} \right). \quad (C-12)$$

### D Commutation matrix code

The following MATLAB code calculates the commutation matrix $K_{m,n}$:

```matlab
1 % Calculates the commutation matrix $K_{m,n}$ such that:
2 % $K_{m,n} \ast \text{vec}(A) = \text{vec}(A')$ where $A$ is dimension $m$ by $n$
3 %
4 % Based on http://m.feng.li/r-tips/r-commutation-matrix
5 function K = Kmn(m,n)
6
7 K = zeros(m*n, m*n);
8 m0 = 1:(m*n);
9
10 N = reshape(m0, m,n)';
11 n0 = N(:);
12
13 for i = 1:(m*n)
14    K(m0(i), n0(i)) = 1;
15 end
```

```