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Formal Relationships 10

Reproductive value, the stable stage distribution, and the sensitivity of the population growth rate to changes in vital rates

Hal Caswell

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Reproductive value, the stable stage distribution, and the sensitivity of the population growth rate to changes in vital rates

Hal Caswell[1]

Abstract

The population growth rate, or intrinsic rate of increase, is the rate of growth that will be achieved by a population with fixed vital rates. The sensitivity of population growth rate to changes in the vital rates can be written in terms of the stable stage or age distribution and the reproductive value distribution. If the vital rate measures the rate of production of one type of individual by another, then the sensitivity of growth rate is proportional to the reproductive value of the destination type and the abundance in the stable stage distribution of the source type. This formal relationship exists in three forms: one for age-classified populations, a second that applies to stage- or age-classified populations, and a third that uses matrix calculus. Each uses a different set of formal demographic techniques; together they provide a relationship that beautifully spans different types of demographic models.

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1. Introduction

A population subject to time-invariant vital rates will (with a few exceptions not of interest here) converge to a stable structure and grow exponentially at a constant rate (the population growth rate, or intrinsic rate of increase). The calculation of the population growth rate from the vital rates is one of the most important accomplishments of formal demography (Sharpe and Lotka 1911: Euler's anticipation of the result in 1760 was not rediscovered until 1970).

If the vital rates change, so will the population growth rate. Perturbation analysis calculates the sensitivity of the growth rate to such changes, and may be useful for several reasons:

(i) To predict the effects of future changes, or to understand the effect of past changes, in the vital rates.
(ii) To determine the fitness consequences of genetic variation in demographic characteristics, and predict the evolutionary outcome of natural selection.
(iii) To compare the results of population policies or, in ecological contexts, of conservation or management strategies.
(iv) To quantify the effect of uncertainty in statistical estimates of the vital rates.

The sensitivities of population growth rate depend on the stable stage (or age) distribution and the reproductive value. In this paper, I present three versions of this formal relationship, each more general than the last. The first (Hamilton 1966), is specific to age-classified models. The second (Caswell 1978) applies to stage-classified as well as age-classified models. The third (Caswell 2007; 2008) is based on matrix calculus and is more flexible than its predecessors. Each approach uses its own mathematical techniques. Since one of the benefits of formal demography is that techniques that arise in one context can later be applied to new problems, I will derive each of these three relationships in turn, discuss their history, and describe some demographic and biodemographic hypotheses that might lead to each kind of calculation. For easier reference, I have collected definitions and relationships needed for the derivation into Section A–C.

A Background: Stable age theory

The following relationships from age-classified stable population theory are used in deriving the relationships (1) and (2).

(A-1)	$\mu(x)$	mortality rate
(A-2)	$\ell(x) = \exp\left(-\int_0^x \mu(a)da\right)$	survivorship
(A-3)	$m(x)$	maternity function
(A-4)	$1 = \int_0^\infty e^{-ra}\ell(a)m(a)da$	Euler-Lotka equation for r
(A-5)	$c(x) = \dfrac{e^{-rx}\ell(x)}{\int_0^\infty e^{-ra}\ell(a)da}$	stable age distribution
(A-6)	$v(x) = \dfrac{e^{rx}}{\ell(x)}\int_x^\infty e^{-ra}\ell(a)m(a)da$	reproductive value
(A-7)	$b = \left[\int_0^\infty e^{-ra}\ell(a)da\right]^{-1}$	birth rate
(A-8)	$\bar{A} = \int_0^\infty a e^{-ra}\ell(a)m(a)da$	mean age of reproduction

B Background: Matrix population models

The relationship (24) for stage-classified models is based on a matrix population model, using the following results regarding eigenvalues, eigenvectors, and stable population theory.

(B-1)	$\mathbf{n}(t)$	population vector at time t
(B-2)	$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$	projection equation
(B-3)	$\mathbf{A} = \left(\ a_{ij}\ \right)$	population projection matrix
(B-4)	$\lambda = \max \mathrm{\mathbf{eig}}(\mathbf{A})$	population growth rate
(B-5)	$\mathbf{A}\mathbf{w} = \lambda\mathbf{w}$	stable stage distribution **w**
(B-6)	$\mathbf{v}^{\mathsf{T}}\mathbf{A} = \lambda\mathbf{v}^{\mathsf{T}}$	reproductive value vector **v**

C Background: Matrix calculus

This section collects results from matrix calculus (Magnus and Neudecker 1988), used in deriving the formal relationship (37).

(C-1)	$\dfrac{d\mathbf{y}}{d\mathbf{x}^{\mathsf{T}}} = \left(\dfrac{dy_i}{dx_j} \right)$	derivative of vector $\mathbf{y}$ w.r.t. vector $\mathbf{x}$
(C-2)	$\mathrm{vec} \begin{pmatrix} a & b \\ c & d \end{pmatrix} = \begin{pmatrix} a & c & b & d \end{pmatrix}^{\mathsf{T}}$	vec operator: stacks columns into a vector
(C-3)	$\dfrac{d\mathrm{vec}\,\mathbf{Y}}{d\mathrm{vec}^{\mathsf{T}}\mathbf{X}}$	derivative of matrix $\mathbf{Y}$ w.r.t. matrix $\mathbf{X}$
(C-4)	$d\mathbf{y} = \mathbf{Q}\mathbf{x} \Longrightarrow \dfrac{d\mathbf{y}}{d\mathbf{x}^{\mathsf{T}}} = \mathbf{Q}$	First identification theorem
(C-5)	$\mathrm{vec}\,(\mathbf{ABC}) = (\mathbf{C}^{\mathsf{T}} \otimes \mathbf{A})\,\mathrm{vec}\,\mathbf{B}$	Roth's theorem
(C-6)	$\dfrac{d\mathbf{y}}{d\mathbf{z}^{\mathsf{T}}} = \dfrac{d\mathbf{y}}{d\mathbf{x}^{\mathsf{T}}} \dfrac{d\mathbf{x}}{d\mathbf{z}^{\mathsf{T}}}$	vector chain rule

2. Age-classified populations

The population growth rate r in an age-classified model is calculated from the Euler-Lotka equation (A-4) as a function of the age schedules of mortality and fertility (Section A).

2.1 The relationship

The sensitivities of r to changes in mortality and fertility at age x are

$$\frac{dr}{d\mu(x)} = \frac{-c(x)v(x)}{b\bar{A}} \tag{1}$$

$$\frac{dr}{dm(x)} = \frac{c(x)}{b\bar{A}} \tag{2}$$

where $c(x)$ is the stable age distribution (A-5), $v(x)$ is the reproductive value (A-6), b is the birth rate (A-7), and $\bar{A}$ is the mean age at reproduction (A-8). That is, the sensitivity of r to a change in mortality at age x is proportional to the product of the reproductive value at age x and the abundance of age x in the stable age distribution. The sensitivity of r to a change in fertility at age x is proportional to the stable age distribution (and the reproductive value at age 0, which, equals 1; see Section 3.). The proportionality constant in each case is the inverse of the product of the birth rate and the mean age of reproduction.

2.2 Derivation

This perturbation analysis of r relies on implicit differentiation of the Euler-Lotka equation (A-4). Let us introduce a perturbation parameter θ to measure the change in mortality or fertility at a specified age.

Writing survival, fertility, and r as functions of θ gives the Euler-Lotka equation

$$1 = \int_0^\infty e^{-r(\theta)a} \ell(\theta, a) m(\theta, a)\, da. \tag{3}$$

Differentiating both sides of (3) with respect to θ gives

$$\begin{aligned} 0 \;=\; & -\frac{dr(\theta)}{d\theta} \int_0^\infty a e^{-r(\theta)a} \ell(\theta, a) m(\theta, a)\, da \\ & + \int_0^\infty e^{-r(\theta)a} \frac{d\ell(\theta, a)}{d\theta} m(\theta, a)\, da \\ & + \int_0^\infty e^{-r(\theta)a} \ell(\theta, a) \frac{dm(\theta, a)}{d\theta}\, da. \end{aligned} \tag{4}$$

Solving (4) for $dr/d\theta$ gives

$$\frac{dr(\theta)}{d\theta} = \frac{1}{\bar{A}} \left(\int_0^\infty e^{-r(\theta)a} \frac{d\ell(\theta, a)}{d\theta} m(\theta, a)\, da + \int_0^\infty e^{-r(\theta)a} \ell(\theta, a) \frac{dm(\theta, a)}{d\theta}\, da \right) \tag{5}$$

where $\bar{A}$ is the mean age of reproduction in the stable population (A-8).

2.2.1 Changes in mortality

If the perturbation affects mortality at age x, we write

$$\mu(\theta, a) = \mu(0, a) + \theta \delta(a - x) \tag{6}$$

where $\delta(x)$ is the unit impulse function.[2] The sensitivity of r to $\mu(x)$ is obtained as the derivative of r with respect to θ, evaluated at $\theta = 0$,

$$\frac{dr}{d\mu(x)} = \left.\frac{dr}{d\theta}\right|_{\theta=0}. \tag{11}$$

Because only mortality is affected by θ

$$\frac{dm(\theta, a)}{d\theta} = 0 \tag{12}$$

$$\frac{d\mu(\theta, a)}{d\theta} = \delta(a - x). \tag{13}$$

From (A-2),

$$\frac{d\ell(\theta, a)}{d\theta} = -e^{-\int_0^a \mu(\theta,s)ds} \int_0^a \delta(a - x)da \tag{14}$$

$$= -\ell(\theta, a)H(a - x). \tag{15}$$

Substituting into (5) and evaluating at $\theta = 0$ gives

$$\frac{dr}{d\mu(x)} = \frac{-1}{\bar{A}} \left(\int_x^\infty e^{-ra}\ell(a)m(a)da \right). \tag{16}$$

---

[2] The unit impulse function, or Dirac delta function, is a generalized function defined by

$$\delta(x) = 0 \qquad x \neq 0 \tag{7}$$

$$\int_{-\infty}^{\infty} \delta(s)ds = 1. \tag{8}$$

The unit impulse is used in signal processing (e.g., Kamen and Heck 1997: p. 7) to represent the limit of a perturbation of unit strength applied over a shorter and shorter time interval. It's most useful properties in our application are

$$\int_{-\infty}^{\infty} \delta(a - x)f(a)da = f(x) \tag{9}$$

and

$$\int_{-\infty}^{x} \delta(s)ds = H(x) \tag{10}$$

where $H(x)$ is the Heaviside function, or unit step function, which satisfies $H(x) = 0$ for $x < 0$ and $H(x) = 1$ for $x > 0$.

The integral in (16) is close to the reproductive value $v(x)$ (A-6); specifically,

$$\int_x^\infty e^{-ra}\ell(a)m(a)da = \ell(x)e^{-rx}v(x). \tag{17}$$

However, from (A-5) and (A-7), $\ell(x)e^{-rx} = c(x)/b$. Making these substitutions into (16) gives the formal relationship (1).

2.2.2 Changes in fertility

If the perturbation affects fertility at age x, we write

$$m(\theta, a) = m(0, a) + \theta\delta(a - x). \tag{18}$$

Because only fertility is affected by θ, $d\mu(\theta, a)/d\theta = 0$ and $dm(\theta, a)/d\theta = \delta(a - x)$. Substituting these into (5) and evaluating the result at $\theta = 0$ gives

$$\frac{dr}{dm(x)} = \frac{1}{\bar{A}} \left(e^{-rx}\ell(x) \right). \tag{19}$$

From (A-5) and (A-7) it can be seen that the numerator is $c(x)/b$, which leads to the formal relationship (2).

2.3 History and perspectives

Hamilton (1966) obtained the relationship (16) in an analysis of the evolution of senescence. From (16) and (2) it is apparent that (provided $r \geq 0$) the magnitudes of the sensitivities of r to mortality and fertility decline with age. These sensitivities measure the selection gradients on age-specific mortality and fertility. Thus Hamilton concluded that the strength of selection against deleterious mutations would decline with their age of action, that small positive effects at early ages could easily compensate for much larger negative effects at later ages, and that the evolution of senescence was therefore inevitable.

In the years that followed Hamilton's paper, several other authors developed perturbation analysis for r, using related methods. Demetrius (1969) used a discrete age-classified model, and Emlen (1970) used Hamilton's results to derive the dynamics of gene frequencies resulting from the selection gradients on age-specific survival and fertility.

Keyfitz (1971), in a remarkable paper, used implicit differentiation to obtain the sensitivity formulae of population growth rate, life expectancy, birth rates, death rates, and the stable age distribution, apparently independently of Hamilton. He noted that the appearance of reproductive value in the sensitivity of r to mortality. Goodman (1971) was apparently the first to note that the sensitivities of r to mortality and fertility could be expressed in terms of the stable age distribution and reproductive value. Arthur (1984) presented an approach based on functional differentiation; it would be interesting to explore the connections between that approach and the matrix calculus methods in Section 4.

When Hamilton's paper appeared in 1966, it was regarded as difficult and esoteric, but it had a great impact. It provided the analytical machinery for examining trade-offs between opposing demographic traits (“antagonistic pleiotropy;" Williams 1957; Rose 1991; Charlesworth 1994). These ideas are fundamental to the analysis of human aging (e.g., Rose 1991; Wachter and Finch Washington, D.C.: National Academy Press; Carey and Tuljapurkar 2003; Baudisch 2005) and, more generally, the analysis of life history evolution in humans and other species (e.g., Charlesworth 1994; Stearns 1992). In the most recent overview of evolutionary biodemography (Vaupel 2010), Hamilton's paper is still one of the foundations of evolutionary life history theory; in the most recent overview of evolutionary biodemography (Vaupel 2010), the paper is one of the first citations.

Hamilton's conclusions about the inevitability of senescence depend on the nature of the perturbations described here by (6) and (18) — that is, additive perturbations to mortality or fertility, respectively. Baudisch (2005; 2008) has pointed out that traits leading to other kinds of perturbations would experience different patterns of selection pressure with age. She examined proportional changes in mortality,

$$\frac{dr}{d\log\mu(x)} = \mu(x)\frac{dr}{d\mu(x)}, \tag{20}$$

additive changes in survival $p(x) = e^{-\mu(x)}$,

$$\frac{dr}{dp(x)} = -\frac{1}{p(x)}\frac{dr}{d\mu(x)}, \tag{21}$$

and proportional changes in survival

$$\frac{dr}{d\log p(x)} = -\frac{dr}{d\mu(x)}. \tag{22}$$

One could also include proportional changes in fertility

$$\frac{dr}{d\log m(x)} = m(x)\frac{dr}{dm(x)}. \tag{23}$$

There is no a priori reason that such traits should not arise in the course of evolution, but they lead to very different conclusions about senescence. In particular, the magnitudes of (20), (21), and (23) may increase, rather than decrease, with age (Baudisch 2005), so Hamilton's conclusion does not apply to such perturbations.

3. Stage-classified populations

Implicit in Hamilton's analysis is the assumption that the vital rates are functions of age. In many cases, they are not. In humans, characteristics such as economic, marital, or health status, or spatial location, may provide important information in addition to age. In other species, the vital rates depend on developmental stage or size more than on age. Such populations are described by stage-classified demographic models, of which the age-classified theory is a special case.

Stage-classified demography can be analyzed using matrix population models (Leslie 1945; Caswell 2001); see Section B. The discrete-time population growth rate λ is the dominant eigenvalue of the population projection matrix $\mathbf{A}$ (guaranteed to be real and positive by the Perron-Frobenius theorem; Caswell 2001). The effects of perturbations on population growth can be approached by looking for the sensitivity of an eigenvalue to changes in the entries of a matrix.

3.1 The relationship

The sensitivity of λ to a change in the entry a_{ij} of $\mathbf{A}$ is (Caswell 1978)

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\mathbf{v}^{\mathsf{T}} \mathbf{w}}, \tag{24}$$

where the stable stage distribution $\mathbf{w}$ and the reproductive value vector $\mathbf{v}$ are the right and left eigenvectors of $\mathbf{A}$. The entry a_{ij} measures the per-capita production of stage i by stage j. The effect of a change in a_{ij} is proportional to the reproductive value of the destination stage and to the abundance of the origin stage in the stable population. This is a generalization of the relationships (1) and (2) obtained from Hamilton's analysis.

3.2 Derivation

The eigenvalue λ is a solution to the characteristic equation of $\mathbf{A}$, which generalizes the Euler-Lotka equation (A-4). Except in special cases it cannot be written down explicitly, making the implicit differentiation approach used by Hamilton impossible. Instead, the relationship (24) is obtained by a perturbation expansion. Suppose that $\mathbf{A}$ is perturbed to

$\mathbf{A}+\Delta\mathbf{A}$. This will result in perturbations of λ and of $\mathbf{w}$, which must satisfy

$$(\mathbf{A}+\Delta\mathbf{A})\,(\mathbf{w}+\Delta\mathbf{w}) = (\lambda+\Delta\lambda)(\mathbf{w}+\Delta\mathbf{w}). \tag{25}$$

Expanding the products, setting second order terms to zero, and remembering that $\mathbf{A}\mathbf{w} = \lambda\mathbf{w}$ gives

$$\mathbf{A}(\Delta\mathbf{w}) + (\Delta\mathbf{A})\mathbf{w} = \lambda(\Delta\mathbf{w}) + (\Delta\lambda)\mathbf{w}. \tag{26}$$

Multiply on the left by $\mathbf{v}^{\mathsf{T}}$ and simplify to obtain

$$(\Delta\lambda)\mathbf{v}^{\mathsf{T}}\mathbf{w} = \mathbf{v}^{\mathsf{T}}(\Delta\mathbf{A})\mathbf{w}. \tag{27}$$

If the perturbation affects only one entry, for example a_{ij}, of $\mathbf{A}$, then

$$\Delta\lambda = \frac{v_i w_j\,(\Delta a_{ij})}{\mathbf{v}^{\mathsf{T}}\mathbf{w}}. \tag{28}$$

Dividing both sides by Δa_{ij} and taking the limit as $\Delta a_{ij} \to 0$ gives the relationship (24).

3.3 Age-classified models as a special case

To compare (24) with Hamilton's results (1) and (2), consider an age-classified matrix (a Leslie matrix) with fertilities F_i in the first row, survival probabilities P_i on the subdiagonal, and zeros elsewhere (Leslie 1945; Keyfitz 1968). In this case (24) simplifies to

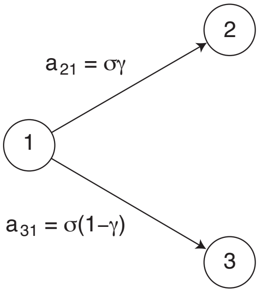
$$\frac{\partial\lambda}{\partial P_i} = \frac{v_{i+1}w_i}{\mathbf{v}^{\mathsf{T}}\mathbf{w}} \tag{29}$$

$$\frac{\partial\lambda}{\partial F_i} = \frac{v_1 w_i}{\mathbf{v}^{\mathsf{T}}\mathbf{w}}. \tag{30}$$

Equation (29) corresponds to (1); the sensitivity is proportional to the product of the reproductive value and the stable stage distribution. Equation (30) corresponds to (2), and shows why reproductive value is apparently missing from (2): reproductive value at birth ($v(0)$ in Hamilton's notation) is scaled to equal 1.

3.4 Sensitivity to lower-level demographic parameters

Figure 1: An example of lower-level parameters appearing in a portion of a life cycle.



Note: Individuals in stage 1 survive with probability σ, and, conditional on survival, move to stage 2 with probability γ and to stage 3 with probability $1 - \gamma$.

The entries of **A** are often functions of other, lower-level parameters. The sensitivity of λ to these parameters is obtained by the chain rule. For example, suppose that stage 1 may contribute individuals to stages 2 or 3 (Figure 1). Write the transition probabilities as

$$a_{21} = \gamma\sigma \tag{31}$$

$$a_{31} = (1-\gamma)\sigma \tag{32}$$

where σ is the survival probability and γ the probability that the individual moves to stage 2, conditional on survival. Then the sensitivities of λ to γ and to σ are given by

$$\frac{d\lambda}{d\sigma} = \frac{\partial\lambda}{\partial a_{21}}\frac{da_{21}}{d\sigma} + \frac{\partial\lambda}{\partial a_{31}}\frac{da_{31}}{d\sigma} \tag{33}$$

$$= \frac{w_1\left[\gamma v_2 + (1-\gamma)v_3\right]}{\mathbf{v}^{\mathsf{T}}\mathbf{w}} \tag{34}$$

$$\frac{d\lambda}{d\gamma} = \frac{\partial\lambda}{\partial a_{21}}\frac{da_{21}}{d\gamma} + \frac{\partial\lambda}{\partial a_{31}}\frac{da_{31}}{d\gamma} \tag{35}$$

$$= \frac{\sigma w_1\left(v_2 - v_3\right)}{\mathbf{v}^{\mathsf{T}}\mathbf{w}}. \tag{36}$$

The sensitivity to survival is proportional to the weighted average of the reproductive values of the destination stages, and the sensitivity to the transition probability γ is proportional to the difference in reproductive value between the destination stages.

3.5 History, perspective, and generalizations

I first encountered this perturbation expansion in the proceedings of an engineering conference (Desoer 1967). Eigenvalue perturbations were of particular interest to engineers in the 1960s as part of a shift from frequency-domain methods to state-space methods in the study of linear systems (Zadeh and Desoer 1963). However, the result dates back to Jacobi (1846), and has been independently rediscovered many times (e.g., Faddeev 1959; Papoulis 1966; Franklin 1968). This perturbation approach has been extended to many other sensitivity problems, including the sensitivity of subdominant eigenvalues and transient behavior, of growth rates in periodic and stochastic environments, of the eigenvectors, and of the spreading speed in biological or demographic invasions (see Caswell 2001: for reviews and references).

4. Sensitivity of growth rate via matrix calculus

Eq. (24) assumes that only a single entry of $\mathbf{A}$ is perturbed, and derivatives with respect to other parameters must be assembled by summing the effects of those parameters on all the entries of $\mathbf{A}$, as in (36). A powerful alternative approach is to treat λ as a scalar function of $\mathbf{A}$, and $\mathbf{A}$ as a matrix-valued function of a vector of lower-level parameters. The mathematical machinery of matrix calculus (Section C, Magnus and Neudecker 1988) makes it possible to do this.

4.1 The relationship

Suppose that $\mathbf{A}$ is a function of a vector $\boldsymbol{\theta}$, of dimension $p \times 1$, of parameters. The derivative of λ with respect to $\boldsymbol{\theta}$ is

$$\frac{d\lambda}{d\boldsymbol{\theta}^{\mathsf{T}}} = \left(\frac{\mathbf{w}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}}{\mathbf{v}^{\mathsf{T}}\mathbf{w}} \right) \left(\frac{d\text{vec}\,\mathbf{A}}{d\boldsymbol{\theta}^{\mathsf{T}}} \right), \tag{37}$$

where $\otimes$ denotes the Kronecker product. In this notation, $d\lambda/d\boldsymbol{\theta}^{\mathsf{T}}$ is a $1 \times p$ vector whose ith entry is $d\lambda/d\theta_i$.

4.2 Derivation

Begin by taking the differential of both sides of (B-5) to give

$$(dA)w + A(dw) = (d\lambda)w + \lambda(dw). \tag{38}$$

where the differential of a matrix or vector is the matrix or vector containing the differentials of the elements. Multiply both sides on the left by $\mathbf{v}^{\mathsf{T}}$ and simplify to obtain

$$(d\lambda)\mathbf{v}^{\mathsf{T}}\mathbf{w} = \mathbf{v}^{\mathsf{T}}(d\mathbf{A})\mathbf{w} \tag{39}$$

Next, apply the vec operator (C-2) to both sides of (39). Since the left side is a scalar, the vec operator has no effect. The right side is a product of three quantities, so Roth's theorem (C-5) implies that

$$d\lambda = \frac{\mathbf{w}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}}{\mathbf{v}^{\mathsf{T}}\mathbf{w}} d\text{vec}\,\mathbf{A} \tag{40}$$

Equation (C-4) (the First Identification Theorem; Magnus and Neudecker 1985), implies that

$$\frac{d\lambda}{d\text{vec}^{\mathsf{T}}\mathbf{A}} = \left(\mathbf{w}^{\mathsf{T}} \otimes \mathbf{v}^{\mathsf{T}}\right). \tag{41}$$

Finally, the chain rule (C-6) gives us the formal relationship (37), for the sensitivity of λ to any vector of parameters. This generalizes the expression (24), but permits easy calculation of the derivatives without having to keep track of summations.

4.3 History and extensions

Modern versions of calculus for matrix equations date back to Dwyer and MacPhail (1948). Several different and not totally compatible approaches have been developed (Nel 1980). The approach adopted here was developed by Magnus and Neudecker (1985) See Magnus and Neudecker (1988) for a complete treatment, and Abadir and Magnus (2005) for a recent introduction).

The matrix calculus approach to perturbation analysis is powerful, because it permits differentiation of scalar-, vector- and matrix-valued functions of scalar-, vector-, or matrix-valued arguments. Thus sensitivity analysis of growth rate is only the beginning of its applications in demography. Recently it has been applied to measures of longevity, net reproductive rate, and generation time (Caswell 2006; 2009b), to nonlinear demographic models (Caswell 2008; 2009a; Verdy and Caswell 2008; Jenouvrier et al. 2010), to stage-structured epidemic models (Klepac and Caswell 2010), and to transient dynamics (Caswell 2007).

5. Conclusion

The three versions of this formal relationship, equations (1 – 2), (24), and (37), use different analytical methods but agree in showing how the sensitivity of population growth rate can be written in terms of the stable stage distribution and the reproductive value. In general, the effect of a change in the rate at which individuals move from stage j to stage i is proportional to the abundance of the origin stage (j) and the reproductive value of the destination stage (i). If a vital rate produces individuals with low reproductive value, or if few individuals are available to experience the change in the rate, the effect on population growth will be small.

In the age-dependent model, the sensitivity of r to changes in fertility (2) appears to lack the dependence on the destination reproductive value; this is because the reproductive value at age 0 is 1. In the stage-dependent model, the reproductive value of the first stage (whatever kind of newborn individual that may represent) is explicitly present in the expression (30).

Each version of this formal relationship uses a different approach to perturbation analysis: implicit differentiation, perturbation expansion, or matrix calculus. Of course, these methods are all related, but each of them is particularly appropriate in its own situations. As a result, perturbation analysis in demography now extends far beyond the population growth rate (e.g., Caswell 2001; 2008; 2009b).

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