

Chapter 9

LTRE Decomposition of the Stochastic Growth Rate



9.1 Introduction

The basic unit of comparative demography is a study that reports the value of some demographic outcome in two populations that differ in a set of vital rates. One challenge of such studies is to account for the difference in outcomes by decomposing that difference into contributions from differences in each of the parameters. It frequently happens that small differences in some parameters make large contributions to the difference in outcomes, and vice-versa.

In some parts of the literature, such studies are called life table response experiment (or LTRE) analyses; versions of this analysis have appeared in Sect. 1.3.1 and Chaps. 2, 4, and 8. The term was introduced by in the context of laboratory studies of the population effects of pollutants, hence the use of the word “experiment” (Caswell 1989). The conditions among which the populations are compared will be called “treatments” here, but there is no restriction to experimental manipulations.

Similar decomposition analyses have been developed independently in ecology and human demography. For example, Pollard’s (1988) study of life expectancy used methods very similar to LTRE analyses of the population growth rate. Horiuchi et al. (2008) developed a method for continuous variables that is essentially identical to that used by ecologists for regression LTRE calculations (Caswell 1996). Canudas Romo (2003) reviews the human demographic literature.

This chapter uses matrix calculus to extend LTRE analysis to stochastic models, by showing how to decompose differences in the stochastic growth rate, $\log \lambda_s$. Because stochastic models include both environmental fluctuations and the vital rate responses to those fluctuations, their structure is richer than that of time-

Chapter 9 is modified from: Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology* 98:324–333. ©Hal Caswell.

invariant models. Stochastic LTRE analysis thus requires a new approach to decomposing these differences. The payoffs, in terms of demographic and biological understanding, are great.

9.2 Decomposition with Derivatives

The familiar LTRE analysis uses derivatives to approximate the contributions of the vital rates to some (vector-valued) outcome ξ (dimension $q \times 1$), as described in Chap. 2. Suppose that ξ depends on a vector θ of vital rates (dimension $p \times 1$), and that observations are available under two treatments, with

$$\theta^{(1)} \longrightarrow \xi^{(1)} \quad (9.1)$$

$$\theta^{(2)} \longrightarrow \xi^{(2)}. \quad (9.2)$$

Using matrix calculus notation, to first order,

$$\xi^{(2)} - \xi^{(1)} \approx \frac{d\xi}{d\theta^T} \left(\theta^{(2)} - \theta^{(1)} \right). \quad (9.3)$$

where the derivative of ξ is evaluated at the mean of the two parameter vectors.

All the contributions to the difference $\xi^{(2)} - \xi^{(1)}$ are contained in a matrix \mathbf{C} (dimension $q \times p$) given by

$$\mathbf{C} = \frac{d\xi}{d\theta^T} \mathcal{D} \left(\theta^{(2)} - \theta^{(1)} \right) \quad (9.4)$$

where the derivative is evaluated at the mean of $\theta^{(1)}$ and $\theta^{(2)}$.

The entry $\mathbf{C}(i, j)$ of the contribution matrix is the contribution of the difference $\Delta\theta_j$ to the difference in $\Delta\xi_i$. The columns and rows of \mathbf{C} give

$$\mathbf{C}(:, j) = \text{contribution of } \Delta\theta_j \text{ to } \Delta\xi \quad (9.5)$$

$$\mathbf{C}(i, :) = \text{contribution of } \Delta\theta \text{ to } \Delta\xi_i. \quad (9.6)$$

The sum over rows of \mathbf{C} is the approximation (9.3) to the treatment effect on ξ

$$\xi^{(2)} - \xi^{(1)} \approx \mathbf{C} \mathbf{1}_p. \quad (9.7)$$

The accuracy of this approximation gives a measure of the adequacy of the first-order assumption. Contributions can be small either because the treatment has little effect on θ_i or because ξ does not respond much to changes in θ_i .

The contribution matrix \mathbf{C} takes advantage of matrix calculus to provide a simple calculation for decomposition of scalar-, vector- or matrix-valued differences.

Studies including more than two treatments or conditions are analyzed by defining a reference parameter vector θ_r and calculating a matrix C_i for treatment i in terms of the parameter difference $\theta_i - \theta_r$. The reference treatment might be the average parameter set, or the parameters for a “control” condition, etc.

9.3 Kitagawa and Keyfitz: Decomposition Without Derivatives

In decomposing differences in the stochastic growth rate, we encounter variables for which the derivatives in (9.3) cannot be calculated. Fortunately, an alternative method for decomposition is available that does not rely on derivatives. It was introduced by Kitagawa (1955) to explore the effects of age-specific death rates and of age distribution on crude death rates. The method was later extended by Keyfitz to decompose differences in age distributions, dependency ratios, and population growth rates into contributions from the entire mortality and fertility schedules (Keyfitz 1968, Section 7.4; Keyfitz and Caswell 2005, Section 10.1). Canudas Romo (2003) summarizes more recent extensions of the approach in demography.

Suppose that ξ depends on two variables, with values (a, b) in Treatment 1 and (A, B) in Treatment 2. Thus

$$\xi^{(1)} = \xi[a, b] \quad (9.8)$$

$$\xi^{(2)} = \xi[A, B]. \quad (9.9)$$

To decompose the treatment effect $\xi[A, B] - \xi[a, b]$ into contributions from $A - a$ and $B - b$, the Kitagawa-Keyfitz method proceeds by exchanging variables between the two treatments and calculating ξ for all possible combinations. The effect of $A - a$, against the background of B , is $\xi[A, B] - \xi[a, B]$. The effect of $A - a$, against the background of b is $\xi[A, b] - \xi[a, b]$. The overall contribution of $A - a$ is obtained by averaging its effect against the two backgrounds:

$$\begin{aligned} C(A - a) &= 1/2 \left(\xi[A, B] - \xi[a, B] \right) \\ &\quad + 1/2 \left(\xi[A, b] - \xi[a, b] \right). \end{aligned} \quad (9.10)$$

Similarly, the contribution of $B - b$ is

$$\begin{aligned} C(B - b) &= 1/2 \left(\xi[A, B] - \xi[A, b] \right) \\ &\quad + 1/2 \left(\xi[a, B] - \xi[a, b] \right). \end{aligned} \quad (9.11)$$

If this appears familiar, it may be because this process of averaging differences across different backgrounds is precisely analogous to the calculation of main effects in a two-way ANOVA (e.g., Steel and Torrie 1960, Section 11.2).

9.4 Stochastic Population Growth

A stochastic model contains two components: a model for the dynamics of the environment and a model for the response of the vital rates to the environment (Cohen 1979; Tuljapurkar 1990; Caswell 2001). I focus here on the stochastic population growth rate, $\log \lambda_s$. Consider a population growing according to

$$\mathbf{n}(t + 1) = \mathbf{A}(t)\mathbf{n}(t) \quad (9.12)$$

where the projection matrix $\mathbf{A}(t)$ is generated by a realization of an ergodic stochastic environment that produces, for every environmental state, a set of vital rates that satisfy certain regularity conditions. Then, the asymptotic long-term growth rate is, with probability one,

$$\log \lambda_s = \lim_{T \rightarrow \infty} \frac{1}{T} \log \left\| \mathbf{A}(T-1) \cdots \mathbf{A}(0)\mathbf{n}_0 \right\| \quad (9.13)$$

(Cohen 1976; Tuljapurkar and Orzack 1980; Tuljapurkar 1990). This growth rate plays a central role in demography and biodemography in stochastic environments, exactly analogous to the role played by the population growth rate λ or $r = \log \lambda$ in stable population theory in constant environments. Cohen (1986) and Lee and Tuljapurkar (1994) have incorporated models of the form (9.12), with the addition of immigration terms, into the context of human population projections, to provide estimates of confidence intervals more rigorous than the “high, medium, low” scenarios usually reported.

The additional component in stochastic environments adds an extra layer of complexity to the LTRE decomposition of the stochastic growth rate (Fig. 9.1). The differences in $\log \lambda_s$ between two treatments is partly due to differences in the environmental dynamics and partly to differences in the vital rates within each environmental state.

In this chapter, I consider the case in which the environment is described by a finite-state Markov chain. Ecological examples include years with our without fire (Silva et al. 1991), years since fire (Caswell and Kaye 2001), years with early or late floods, or with high or low precipitation (Smith et al. 2005) and years with good or poor sea ice conditions (Hunter et al. 2010; Jenouvrier et al. 2009b). The Markovian environment case also includes the situation where the environment is modelled implicitly by selecting randomly from a set of empirically-measured matrices (e.g., Bierzychudek 1982; Cohen et al. 1983; Jenouvrier et al. 2009a). Let $u(t)$ be the state of the environment at time t . The environmental dynamics are determined by the Markov chain transition matrix \mathbf{P} , where $p_{ij} = P[u(t+1) = i | u(t) = j]$.

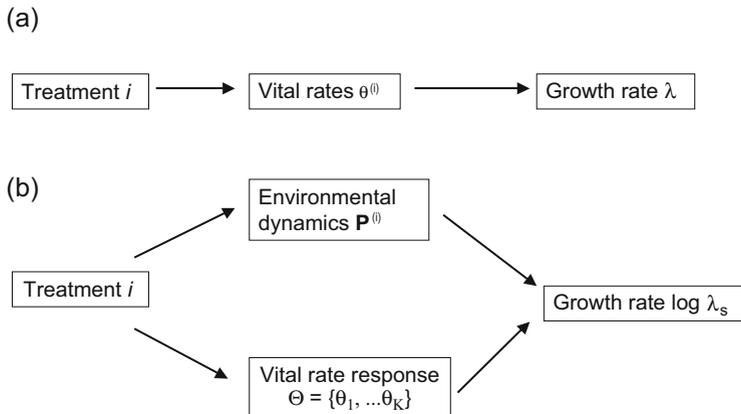


Fig. 9.1 The determination of population growth rate in (a) time-invariant and (b) stochastic models. The deterministic growth rate λ is defined by a set of vital rates, which are determined by the environment (“treatment”). The stochastic growth rate $\log \lambda_s$ requires an additional model for the stochastic dynamics of the environment and a function giving the response of the vital rates to the state of the environment

The second part of the model is the response of the vital rates to the environment. Let θ be a vector of parameters that determine the projection matrix \mathbf{A} . The vectors $\theta_1, \dots, \theta_K$ correspond to environmental states $1, \dots, K$. I will write the entire set of vital rates as

$$\Theta = \{\theta_1, \dots, \theta_K\}. \tag{9.14}$$

We write $\mathbf{A}(t) = \mathbf{A}[\theta(t)]$, and the stochastic growth rate (9.13) becomes

$$\log \lambda_s [\mathbf{P}, \Theta] = \lim_{T \rightarrow \infty} \frac{1}{T} \log \left\| \mathbf{A}[\theta(T-1)] \cdots \mathbf{A}[\theta(0)] \mathbf{n}_0 \right\| \tag{9.15}$$

where $\theta(t)$ is the parameter vector created by the environmental state $u(t)$. I have written $\log \lambda_s$ as an explicit function of \mathbf{P} and Θ to emphasize that it depends on both the environment and the vital rate response.

9.4.1 Environment-Specific Sensitivities

The sensitivity of $\log \lambda_s$ to the vital rates was given by Tuljapurkar (1990). For the LTRE analysis, we require the derivatives of $\log \lambda_s$ with respect to the parameters in each state of the environment; i.e., to each of the vectors θ_i in Θ . These environment-specific sensitivities were given by Caswell (2005) and independently by Horvitz et al. (2005), and have been applied by Gervais et al. (2006), Aberg

et al. (2009), and Svensson et al. (2009). Rewriting Tuljapurkar's (1990) formula in matrix calculus notation yields the derivative of $\log \lambda_s$ with respect to the vital rate vector in environment i :

$$\left. \frac{d \log \lambda_s}{d\boldsymbol{\theta}^\top} \right|_{u=i} = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=0}^{T-1} J_t \frac{[\mathbf{w}(t)^\top \otimes \mathbf{v}(t+1)^\top]}{R_t \mathbf{v}^\top(t+1) \mathbf{w}(t+1)} \frac{d \text{vec } \mathbf{A}[\boldsymbol{\theta}(t)]}{d\boldsymbol{\theta}^\top}. \quad (9.16)$$

This is the stochastic analogue of the expression (3.46) in Chap. 3, for the sensitivity of the deterministic growth rate. The vectors $\mathbf{w}(t)$ and $\mathbf{v}(t)$ are the stochastic analogues of the right and left eigenvectors of a deterministic model, and R_t is the growth of total population size from t to $t+1$. See Caswell (2001, Section 14.4) for a step-by-step algorithm for the calculation.

To make sensitivity environment-dependent, J_t is an indicator variable, defined as

$$J_t = \begin{cases} 1 & \text{if } u(t) = i \\ 0 & \text{otherwise} \end{cases} \quad (9.17)$$

If the parameters $\boldsymbol{\theta}$ consist of the elements of \mathbf{A} , then $d \text{vec } \mathbf{A} / d\boldsymbol{\theta}^\top = \mathbf{I}$, where \mathbf{I} is the identity matrix. If $\boldsymbol{\theta}$ contains lower-level parameters, then $d \text{vec } \mathbf{A} / d\boldsymbol{\theta}^\top$ contains the derivatives of \mathbf{A} with respect to these parameters.

9.5 LTRE Decomposition Analysis for $\log \lambda_s$

Suppose now that we have two treatments, and want to decompose the difference,

$$\log \lambda_s^{(2)} - \log \lambda_s^{(1)} = \log \lambda_s [\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(2)}] - \log \lambda_s [\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(1)}] \quad (9.18)$$

into contributions. This difference compares growth in treatment 2 to growth in treatment 1. Treatment 1, the reference treatment, could be a control in a manipulative experiment, or some other specific condition of interest (as in the example to be considered below), or an average over treatments in a factorial experiment.

The treatment effect on $\log \lambda_s$ in (9.18) depends on both the differences in environmental dynamics (captured in the transition matrices $\mathbf{P}^{(1)}$ and $\mathbf{P}^{(2)}$) and the differences in the vital rate responses (captured in the parameter arrays $\boldsymbol{\Theta}^{(1)}$ and $\boldsymbol{\Theta}^{(2)}$). Because $\log \lambda_s$ is calculated numerically from (9.15) by simulation, it cannot be differentiated¹ with respect to \mathbf{P} , so we will use the Kitagawa-Keyfitz

¹Well, not by me. But see Steinsaltz et al. (2011) for a rigorous development of the sensitivity analysis of stochastic growth rates that includes the effects of changes in the entries of \mathbf{P} .

decomposition for the environmental dynamics contribution, and environment-specific derivatives (9.16) for the vital rate response contributions

Let us consider three cases: the case where only the vital rate responses differ, the case where only the environmental dynamics differ, and finally the case where both differ.

9.5.1 Case 1: Vital Rates Differ, Environments Identical

Consider two treatments that affect the vital rate responses but not the environmental dynamics. For example, one might want to compare low and high fertility sites subjected to a common fire frequency. The transition matrix \mathbf{P} is identical in the two sites, but the vital rates differ. The stochastic growth rates are

$$\log \lambda_s^{(1)} = \log \lambda_s \left[\mathbf{P}, \boldsymbol{\Theta}^{(1)} \right] \quad (9.19)$$

$$\log \lambda_s^{(2)} = \log \lambda_s \left[\mathbf{P}, \boldsymbol{\Theta}^{(2)} \right]. \quad (9.20)$$

The difference in $\log \lambda_s$ is composed of contributions from vital rate differences in each state of the environment. To first order,

$$\log \lambda_s^{(2)} - \log \lambda_s^{(1)} \approx \sum_{i=1}^K \left(\frac{\partial \log \lambda_s}{\partial \boldsymbol{\theta}^T} \Big|_{u=i} \right) \left(\boldsymbol{\theta}_i^{(2)} - \boldsymbol{\theta}_i^{(1)} \right) \quad (9.21)$$

where the derivatives are environment-specific sensitivities (9.16), and are evaluated at the mean of $\boldsymbol{\Theta}^{(1)}$ and $\boldsymbol{\Theta}^{(2)}$. The i th term of the summation in (9.21) is the contribution of differences in the i th environment. These can be written as the elements of a contribution matrix (dimension $1 \times p$)

$$\mathbf{C}(\boldsymbol{\theta}_i) = \frac{\partial \log \lambda_s}{\partial \boldsymbol{\theta}^T} \Big|_{u=i} \mathcal{D} \left(\boldsymbol{\theta}_i^{(2)} - \boldsymbol{\theta}_i^{(1)} \right) \quad i = 1, \dots, K. \quad (9.22)$$

9.5.2 Case 2: Vital Rates Identical, Environments Differ

Now consider two treatments that affect the environmental dynamics (given by $\mathbf{P}^{(1)}$ and $\mathbf{P}^{(2)}$) but not the vital rate responses. For example, a comparison of population growth before and after implementing a fire control strategy that changes the frequency of fire, but has no effect on how the vital rates respond to fire. The stochastic growth rates are

$$\log \lambda_s^{(1)} = \log \lambda_s \left[\mathbf{P}^{(1)}, \boldsymbol{\Theta} \right] \quad (9.23)$$

$$\log \lambda_s^{(2)} = \log \lambda_s \left[\mathbf{P}^{(2)}, \boldsymbol{\Theta} \right]. \quad (9.24)$$

The matrices $\mathbf{P}^{(1)}$ and $\mathbf{P}^{(2)}$ may differ in their long-term frequencies of environmental states. Those long-term frequencies are given by the stationary distributions, i.e., the right eigenvector $\boldsymbol{\pi}$ corresponding to the dominant eigenvalue of \mathbf{P} (which always equals 1), scaled so that $\boldsymbol{\pi}$ sums to 1. The same frequency of environmental states, however, can be obtained from processes with different autocorrelation patterns, from negative autocorrelation (where states tend to alternate) to positive autocorrelation (characterized by long runs of the same state; see Caswell and Kaye (2001, Fig. 2) for an example). So, $\mathbf{P}^{(1)}$ and $\mathbf{P}^{(2)}$ may differ in their stationary distributions, autocorrelation patterns, or both. To separate the contributions from these, using the Kitagawa-Keyfitz decomposition, we construct a Markov chain with the same stationary distribution $\boldsymbol{\pi}$ as \mathbf{P} , but in which successive environmental states are independent, and hence there is no autocorrelation. This chain has the transition matrix

$$\mathbf{Q} = \boldsymbol{\pi} \mathbf{1}^T \quad (9.25)$$

where $\mathbf{1}$ is a vector of ones. Because the next state is independent of the previous state, and the same matrix is applied at each time, this process is called “independent and identically distributed,” and abbreviated “iid.”

The contribution to $\log \lambda_s^{(2)} - \log \lambda_s^{(1)}$ of differences in \mathbf{P} is

$$C(\mathbf{P}) = \log \lambda_s \left[\mathbf{P}^{(2)}, \boldsymbol{\Theta} \right] - \log \lambda_s \left[\mathbf{P}^{(1)}, \boldsymbol{\Theta} \right]. \quad (9.26)$$

The contribution of the difference in the iid part of the environment is

$$C(\mathbf{Q}) = \log \lambda_s \left[\mathbf{Q}^{(2)}, \boldsymbol{\Theta} \right] - \log \lambda_s \left[\mathbf{Q}^{(1)}, \boldsymbol{\Theta} \right]. \quad (9.27)$$

The contribution of differences in environmental autocorrelation, denoted by $C(\mathbf{R})$, is obtained by subtraction;

$$C(\mathbf{R}) = C(\mathbf{P}) - C(\mathbf{Q}). \quad (9.28)$$

9.5.3 Case 3: Vital Rates and Environments Differ

Finally, consider two treatments that differ in both the environmental dynamics ($\mathbf{P}^{(1)}$ and $\mathbf{P}^{(2)}$) and the vital rate responses ($\boldsymbol{\Theta}^{(1)}$ and $\boldsymbol{\Theta}^{(2)}$). The stochastic growth rates are

$$\log \lambda_s^{(1)} = \log \lambda_s \left[\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(1)} \right] \quad (9.29)$$

$$\log \lambda_s^{(2)} = \log \lambda_s \left[\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(2)} \right]. \quad (9.30)$$

Our goal is to decompose $\log \lambda_s^{(2)} - \log \lambda_s^{(1)}$ into contributions from the differences in the stationary environmental frequencies ($C(\mathbf{Q})$), in the autocorrelation pattern ($C(\mathbf{R})$), and in the vital rates in each environmental state ($C(\boldsymbol{\theta}_1), \dots, C(\boldsymbol{\theta}_K)$). The decomposition analysis proceeds in three steps.

1. Write the contributions of the environmental differences using the Kitagawa-Keyfitz method

$$C(\mathbf{P}) = \frac{1}{2} \left(\log \lambda_s [\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(2)}] - \log \lambda_s [\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(2)}] \right. \\ \left. + \log \lambda_s [\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(1)}] - \log \lambda_s [\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(1)}] \right) \quad (9.31)$$

$$C(\mathbf{Q}) = \frac{1}{2} \left(\log \lambda_s [\mathbf{Q}^{(2)}, \boldsymbol{\Theta}^{(2)}] - \log \lambda_s [\mathbf{Q}^{(1)}, \boldsymbol{\Theta}^{(2)}] \right. \\ \left. + \log \lambda_s [\mathbf{Q}^{(2)}, \boldsymbol{\Theta}^{(1)}] - \log \lambda_s [\mathbf{Q}^{(1)}, \boldsymbol{\Theta}^{(1)}] \right) \quad (9.32)$$

$$C(\mathbf{R}) = C(\mathbf{P}) - C(\mathbf{Q}) \quad (9.33)$$

Each of $C(\mathbf{P})$, $C(\mathbf{Q})$, and $C(\mathbf{R})$ is a scalar.

2. Write the contributions of the vital rate differences using the Kitagawa-Keyfitz method

$$C(\boldsymbol{\Theta}) = \frac{1}{2} \left\{ \log \lambda_s [\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(2)}] - \log \lambda_s [\mathbf{P}^{(2)}, \boldsymbol{\Theta}^{(1)}] \right\} \\ + \frac{1}{2} \left\{ \log \lambda_s [\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(2)}] - \log \lambda_s [\mathbf{P}^{(1)}, \boldsymbol{\Theta}^{(1)}] \right\} \quad (9.34)$$

$C(\boldsymbol{\Theta})$ is a scalar, summing the effects of differences in all of the parameter responses at all states of the environment. It is decomposed further in the next step:

3. Use the environment-specific derivatives of $\log \lambda_s$ to decompose each term in (9.34) into contributions from the vital rates in each environment, using (9.22)

$$\mathbf{C}(\boldsymbol{\theta}_i) = \frac{1}{2} \left(\frac{\partial \log \lambda_s [\mathbf{P}^{(2)}, \bar{\boldsymbol{\Theta}}]}{\partial \boldsymbol{\theta}^\top} \Big|_{u=i} \right) \mathcal{D} \left(\boldsymbol{\theta}_i^{(2)} - \boldsymbol{\theta}_i^{(1)} \right) \\ + \frac{1}{2} \left(\frac{\partial \log \lambda_s [\mathbf{P}^{(1)}, \bar{\boldsymbol{\Theta}}]}{\partial \boldsymbol{\theta}^\top} \Big|_{u=i} \right) \mathcal{D} \left(\boldsymbol{\theta}_i^{(2)} - \boldsymbol{\theta}_i^{(1)} \right) \quad i = 1, \dots, K \quad (9.35)$$

for $i = 1, \dots, K$, with the derivatives evaluated at $\bar{\Theta}$, the mean of the vital rates in the two treatments being compared. The matrix $\mathbf{C}(\theta_i)$ is $(1 \times p)$ vector, whose entries give the contributions to the differences in $\log \lambda_s$ from each of the vital rates in environment i .

The total contribution of the parameter differences given in (9.34) is

$$\mathbf{C}(\Theta) = \sum_{i=1}^K \mathbf{C}(\theta_i) \mathbf{1}_p. \quad (9.36)$$

These calculations are easily implemented by writing subroutines to calculate $\log \lambda_s$ and the environment-specific sensitivities given a transition matrix and a set of parameters. The accuracy of the approximations involved can be checked by comparing

$$\log \lambda_s^{(2)} - \log \lambda_s^{(1)} \stackrel{?}{\approx} \mathbf{C}(\mathbf{Q}) + \mathbf{C}(\mathbf{R}) + \sum_{i=1}^K \mathbf{C}(\theta_i) \mathbf{1}_p. \quad (9.37)$$

9.6 An Example: Fire and an Endangered Plant

I know of no comparative studies of stochastic population growth that include differences in both the environmental dynamics and the vital rate responses, so here is an artificial example, based on a model for an endangered plant, *Lomatium bradshawii*, in a stochastic fire environment (Caswell and Kaye 2001). *L. bradshawii* (Apiaceae) is a polycarpic herbaceous perennial plant. It exists in only a few isolated populations in prairies of Oregon and Washington. These habitats were, until recent times, subject to natural and anthropogenic fires, to which *L. bradshawii* seems to have adapted. Fires increase plant size and seedling recruitment, but the effect fades within a few years. Populations in recently burned areas have higher growth rates and lower probabilities of extinction than unburned populations. For more information, see Pendergrass et al. (1999), Caswell and Kaye (2001), and Kaye et al. (2001).

A stochastic demographic model for *L. bradshawii* was developed by Caswell and Kaye (2001), based on data from an experimental burning study. Individuals were classified into six stages based on size and reproductive status: yearlings, small and large vegetative plants, and small, medium, and large reproductive plants. The environment was classified into four states defined by the time since the most recent fire: the year of a fire and 1, 2, and 3+ years post-fire, and vital rates were estimated in each of these environmental states. The matrices are given in Caswell and Kaye (2001).

Populations were studied in two sites: Fisher Butte (FB) and Rose Prairie (RP) in western Oregon. The two sites differed in quality for *L. bradshawii*, with RP

Table 9.1 The population growth rate λ calculated from the environment-specific matrices $\mathbf{A}[\theta_i]$ for *L. bradshawii*. (From Caswell and Kaye 2001)

	Fisher Butte	Rose Prairie
Years post-fire	λ	λ
0	1.020	1.155
1	0.984	1.118
2	0.662	0.483
≥ 3	0.869	0.906

superior to FB. Population growth rates were generally higher at RP than at FP (Table 9.1), and the stochastic growth rate was higher in RP than FB at any fire frequency. The critical fire frequency required to maintain *L. bradshawii* populations was about 0.8–0.9 at FB, but only 0.4–0.5 at RP. The causes of the differences between the sites are not known (Pendergrass et al. 1999).

9.6.1 The Stochastic Fire Environment

The model for environmental dynamics is a two-state Markov chain for fires (each year is either fire or no fire). This generates a four-state Markov chain for the environmental states (0, 1, 2, and 3 or more years post-fire). Let f be the long-term frequency of fire, and ρ the temporal autocorrelation coefficient of the fire process (the magnitude of ρ determines the rate of decay of correlation as time increases, the sign of ρ determines whether the correlation is of one sign, or oscillates). In the two-state fire model, the probability of fire in year $t + 1$ if there was no fire in year t is $q = f(1 - \rho)$. The probability of a fire if there was a fire in year t is $p = q + \rho$ (see Caswell 2001, Section 14.1). The resulting transition matrix for the four environmental states is

$$\mathbf{P} = \begin{pmatrix} p & q & q & q \\ 1 - p & 0 & 0 & 0 \\ 0 & 1 - q & 0 & 0 \\ 0 & 0 & 1 - q & 1 - q \end{pmatrix}. \tag{9.38}$$

If $\rho < 0$, f must satisfy

$$\frac{-\rho}{1 - \rho} \leq f \leq \frac{1}{1 - \rho} \tag{9.39}$$

in order to keep probabilities bounded between 0 and 1. See Caswell and Kaye (2001). Note that even if the fire process is iid, so that $\rho = 0$, the environmental process given by (9.38) is not iid.

9.6.2 LTRE Analysis

There is no information on differences in fire dynamics at the two sites, so Caswell and Kaye (2001) studied the response of $\log \lambda_s$ to the frequency and autocorrelation of fires. Here, we use stochastic LTRE analysis to decompose the differences in $\log \lambda_s$ in three hypothetical scenarios of environmental differences. I will use the matrix entries as the vital rates θ , there being no natural lower-level parameterization in this model. MATLAB code for the calculations is available as an appendix to Caswell (2010).

The stochastic growth rate $\log \lambda_s$ increases with fire frequency for both species. The RP site has a growth advantage, with $\log \lambda_s^{(RP)} > \log \lambda_s^{(FB)}$ at all fire frequencies. The RP advantage, measured by $\log \lambda_s^{(RP)} - \log \lambda_s^{(FB)}$ increases from ≈ 0.02 when $f = 0$ to ≈ 0.13 when $f = 1$.

Differences in vital rates and environmental transitions (Case 3) Suppose that the two sites differ in both environmental dynamics and vital rate responses, with fire frequencies, autocorrelations, and resulting stochastic growth of

	FB	RP
f	0.5	0.7
ρ	-0.5	0.5
$\log \lambda_s$	-0.043	0.081

In this hypothetical scenario, the FB population tends to experience alternating years with and without fires; in RP, there is a tendency for long runs of years with and without fires. For additional scenarios, see Caswell (2010).

To decompose the treatment effect $\log \lambda_s^{(RP)} - \log \lambda_s^{(FB)}$, we construct the Markov chain transition matrices from (9.38), and calculate the stationary distributions $\pi^{(RP)}$ and $\pi^{(FB)}$ as eigenvectors of \mathbf{P} . For each site, we generate the iid transition matrix \mathbf{Q} from (9.25), and compute the contributions $C(\mathbf{P})$ from (9.31), $C(\mathbf{Q})$ from (9.32), and $C(\mathbf{R})$ from (9.33). Then we compute the environment-specific sensitivities of $\log \lambda_s$ from (9.16), for both $\mathbf{P}^{(RP)}$ and $\mathbf{P}^{(FB)}$, and use these to calculate the contributions $C(\theta_i)$ of the vital rates in each environmental state, using (9.35). Finally, we sum the $C(\theta_i)$ to obtain the integrated effect of all vital rate differences in each environment.

Figure 9.2 shows these contributions. Most of the growth rate advantage of the RP site can be attributed to an RP advantage in $\mathbf{A}[\theta_1]$ and $\mathbf{A}[\theta_2]$ (the year of a fire and the year immediately following a fire). The difference in the long-term frequency of environmental states, and the differences in autocorrelation patterns, make relatively little contribution.

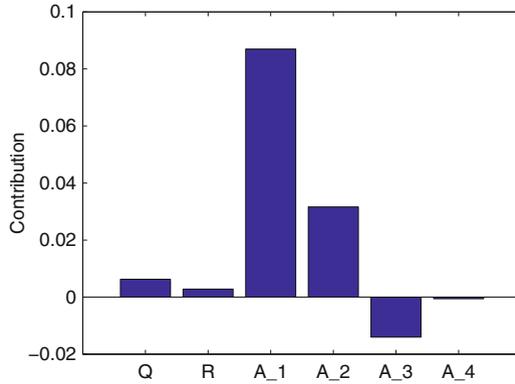


Fig. 9.2 The contributions of the iid component of the environment (**Q**), the autocorrelated component of the environment (**R**), and the projection matrix entries in each environmental state (**A₁, . . . A₄**) to the difference in the stochastic growth rate $\log \lambda_s$ between the Rose Prairie (RP) and Fisher Butte (FB) populations of *Lomatium bradshawii*. Calculations assume fire frequencies of 0.5 for FB and 0.7 for RP, and autocorrelations $\rho = -0.5$ for FB and $\rho = 0.5$ for RP

The accuracy of the approximations involved in the LTRE analysis is good. The sum of the contributions in Fig. 9.2 is 0.1192, while the actual difference in $\log \lambda_s$ is 0.1219 (an accuracy of 98%).

Alternatively, suppose that some kind of fire prevention program in the RP site reduced the fire frequency to $f = 0.1$ (well below the critical threshold for persistence), but a fire management program increased the fire frequency in the FP site to $f = 0.9$.

	FB	RP
f	0.9	0.1
ρ	0.0	0.0
$\log \lambda_s$	0.027	-0.113

Now $\log \lambda_s^{(FB)} > \log \lambda_s^{(RP)}$, despite the general advantage in vital rates of RP over FB in most environmental states. Figure 9.3 presents the contributions to $\Delta \log \lambda_s$ from differences in fire frequency, autocorrelation, and vital rates, and shows how the contributions of the vital rate differences are, in this case, overwhelmed by the RP disadvantage due to the stationary distribution of the environment.

The sum of the contributions in Fig. 9.3 is -0.1326 , while the actual difference in $\log \lambda_s$ is -0.1395 (an accuracy of 95%, even with a very large difference in growth rate).

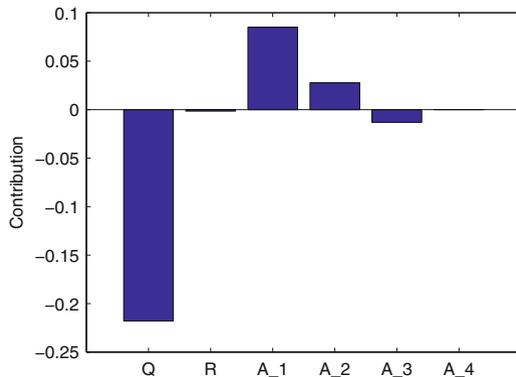


Fig. 9.3 The contributions of the iid component of the environment (**Q**), the autocorrelated component of the environment (**R**), and the matrix entries in each environmental state (**A**₁, . . . **A**₄) to the difference in the stochastic growth rate $\log \lambda_s$ between the Rose Prairie (RP) and Fisher Butte (FB) populations of *Lomatium bradshawii*. Calculations assume fire frequencies of 0.9 for FB and 0.1 for RP, and autocorrelation $\rho = 0$ for both populations

9.7 Discussion

This application of matrix calculus provides a general framework for decomposition analysis of the stochastic growth rate in Markovian environments. It is a direct generalization of the familiar LTRE approaches for time-invariant and periodic models, but combined with the powerful Kitagawa-Keyfitz decomposition. Comparative studies of the stochastic growth rate require additional data on the stochastic dynamics of the environment, beyond that needed for time-invariant models (Fig. 9.1). Many stochastic studies present conditional results; for example, the study of *L. bradshawii* provides $\log \lambda_s$ as a function of f , ρ , and Θ , but does not estimate the value of $\log \lambda_s$ actually exhibited in either of the two sites. To do so would require long-term data on the stochastic environment, which is hard to come by. However, such information may possibly be extracted from historical data (e.g., Smith et al. 2005; Lawler et al. 2009), or projected from climate models (Hunter et al. 2010; Jenouvrier et al. 2009b).

The methods presented here are not limited to Markovian environments in which the environmental states have an interpretation (years since fire, flood conditions, etc.). They can also be used when matrices are randomly selected from a series collected over time (e.g., the early study of Bierzychudek (1982) based on two yearly matrices, or the study by Jenouvrier et al. (2009b) based on 44 years of matrices for emperor penguins). Although such models are indeed Markov chains, if years are simply a random sample of environmental variation, then it is of little interest to know the contribution of vital rate differences in, say, 1988 compared to 1989 or 1987. In these models, the mean and variance of the vital rates may be of more interest. Davison et al. (2010), drawing on the stochastic elasticity results of

Tuljapurkar et al. (2003), have presented an approach to LTRE analysis in terms of the contributions of differences in the mean and the variance of the vital rates. That method nicely complements the approach presented here.

In the analysis of *Lomatium bradshawii*, even large differences in environmental autocorrelation made small contributions to treatment effects on $\log \lambda_s$. This is not surprising, given the generally small impact of changes in autocorrelation on the stochastic growth rate in this model (Caswell and Kaye 2001). It is, however, not guaranteed. Given the proper interaction between environmental states and the stage structure, autocorrelation can have dramatic impacts on the growth rate (Caswell 2001, Example 14.1). How often this happens in nature will only be revealed by further comparative studies.

Changing focus from plants in a fluctuating fire environment to human populations projected in response to stochastic fluctuations in mortality and fertility (e.g., Tuljapurkar 1992; Lee and Tuljapurkar 1994), there are possibilities for applying this approach to population projections. However, such attempts will be challenging because the stochastic environments are not stationary, and the interest is not in asymptotic stochastic growth, but in short term transient dynamics. A combination of the transient analyses in Chap. 7 with the decomposition approach here might yield interesting results.

Bibliography

- Aberg, P., C. J. Svensson, H. Caswell, and H. Pavia. 2009. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. *Ecological Modelling* **220**:605–610.
- Bierzychudek, P. 1982. The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs* **52**:335–351.
- Canudas Romo, V. 2003. Decomposition methods in demography. Population Studies, Rozenberg Publishers, Amsterdam, Netherlands.
- Caswell, H. 1989. Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling* **46**:221–237.
- Caswell, H., 1996. Demography meets ecotoxicology: untangling the population level effects of toxic substances. Pages 255–292 in M. C. Newman and C. H. Jagoe, editors. *Ecotoxicology: a hierarchical treatment*. Lewis Publishers, Boca Raton, Florida.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. 2nd edition. Sinauer Associates, Sunderland, MA.
- Caswell, H. 2005. Sensitivity analysis of the stochastic growth rate: three extensions. *Australian and New Zealand Journal of Statistics* **47**:75–85.
- Caswell, H. 2010. Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology* **98**:324–333.
- Caswell, H., and T. N. Kaye. 2001. Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii*) in a dynamic fire regime. *Advances in Ecological Research* **32**:1–51.
- Cohen, J. E. 1976. Ergodicity of age structure in populations with Markovian vital rates I: countable states. *Journal of the American Statistical Association* **71**:335–339.
- Cohen, J. E. 1979. Ergodic theorems in demography. *Bulletin of the American Mathematical Society* **1**:275–295.

- Cohen, J. E. 1986. Population forecasts and confidence intervals for Sweden: A comparison of model-based and empirical approaches. *Demography* **23**:105–126.
- Cohen, J. E., S. W. Christensen, and C. P. Goodyear. 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. *Canadian Journal of Fisheries and Aquatic Sciences* **40**:2170–2183.
- Davison, R., H. Jacquemyn, D. Adriaens, O. Honnay, H. De Kroon, and S. Tuljapurkar. 2010. Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. *Journal of Ecology* **98**:255–267.
- Gervais, J. A., C. M. Hunter, and R. G. Anthony. 2006. Interactive effects of prey and p,p' -DDE on burrowing owl population dynamics. *Ecological Applications* **16**:666–677.
- Horiuchi, S., J. R. Wilmoth, and S. D. Pletcher. 2008. A decomposition method based on a model of continuous change. *Demography* **45**:785–801.
- Horvitz, C. C., S. Tuljapurkar, and J. B. Pascarella. 2005. Plant-animal interactions in random environments: habitat-stage elasticity, seed predators, and hurricanes. *Ecology* **86**:3312–3322.
- Hunter, C. M., H. Caswell, M. C. Runge, E. V. Regehr, S. C. Amstrup, and I. Stirling. 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* **91**:2883–2897.
- Jenouvrier, S., C. Barbraud, H. Weimerskirch, and H. Caswell. 2009a. Limitation of population recovery: a stochastic approach to the case of the emperor penguin. *Oikos* **118**:1292–1298.
- Jenouvrier, S., H. Caswell, C. Barbraud, M. Holland, J. Strøve, and H. Weimerskirch. 2009b. Demographic models and IPCC climate projections predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences* **106**:1844–1847.
- Kaye, T. N., K. L. Pendergrass, K. Finley, and J. B. Kauffman. 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications* **11**:1366–1380.
- Keyfitz, N. 1968. *Introduction to the Mathematics of Population*. Addison-Wesley, Reading, Massachusetts, USA.
- Keyfitz, N., and H. Caswell. 2005. *Applied mathematical demography*. 3rd edition. Springer, New York, New York.
- Kitagawa, E. M. 1955. Components of a difference between two rates. *Journal of the American Statistical Association* **50**:1168–1194.
- Lawler, R. L., H. Caswell, A. F. Richard, J. Ratsirarson, R. E. Dewar, and M. Schwartz. 2009. Population dynamics of Verreaux's sifaka in a stochastic rainfall environment. *Oecologia* **161**:491–504.
- Lee, R. D., and S. Tuljapurkar. 1994. Stochastic population forecasts for the United States: Beyond high, medium, and low. *Journal of the American Statistical Association* **89**:1175–1189.
- Pendergrass, K. L., P. M. Miller, J. B. Kauffman, and T. N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. *Ecological Applications* **9**:1420–1429.
- Pollard, J. H. 1988. On the decomposition of changes in expectation of life and differentials in life expectancy. *Demography* **25**:265–276.
- Silva, J. F., J. Raventos, H. Caswell, and M. C. Trevisan. 1991. Population responses to fire in a tropical savanna grass *Andropogon semiberbis*: a matrix model approach. *Journal of Ecology* **79**:345–356.
- Smith, M., H. Caswell, and P. Mettler-Cherry. 2005. Stochastic flood and precipitation regimes and the population dynamics of a threatened floodplain plant. *Ecological Applications* **15**:1036–1052.
- Steel, R. G. D., and J. H. Torrie. 1960. *Principles and procedures of statistics*. McGraw-Hill, New York, New York.
- Steinsaltz, D., S. Tuljapurkar, and C. Horvitz. 2011. Derivatives of the stochastic growth rate. *Theoretical Population Biology* **80**:1–15.
- Svensson, C. J., H. Pavia, and P. Aberg. 2009. Robustness of life history of the brown seaweed *Ascophyllum nodosum* (Fucales, Phaeophyceae) across large scales: effects of spatially and temporally induced variability on population growth. *Marine Biology* **156**:1139–1148.

- Tuljapurkar, S. 1990. *Population Dynamics in Variable Environments*. Springer-Verlag, New York, New York.
- Tuljapurkar, S. 1992. Stochastic population forecasts and their uses. *International Journal of Forecasting* **8**:385–391.
- Tuljapurkar, S., C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. *American Naturalist* **162**:489–502.
- Tuljapurkar, S., and S. H. Orzack. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. *Theoretical Population Biology* **18**:314–342.

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

