

# Chapter 7

## Transient Population Dynamics



### 7.1 Introduction

Short-term, transient population dynamics can differ in important ways from long-term asymptotic dynamics. Just as perturbation analysis (sensitivity and elasticity) of the asymptotic growth rate reveals the effects of the vital rates on long-term growth (Chap. 3), the perturbation analysis of transient dynamics can reveal the determinants of short-term patterns. This chapter presents a comprehensive approach to transient sensitivity analysis that applies to linear time-invariant, time-varying, subsidized, stochastic, nonlinear, and spatial models.

In a constant environment, once a population converges to its stable stage structure, it grows exponentially at a constant rate  $\lambda$ . However, depending on initial conditions, short-term transient dynamics can differ from the asymptotic dynamics. It has long been recognized that a focus on  $\lambda$  alone can obscure these important transient effects (e.g., Lotka 1939; Coale 1972). There have been attempts to develop transient sensitivity analyses using all the eigenvalues of the projection matrix (Fox and Gurevitch 2000), but these are complicated to calculate and limited in application. Matrix calculus allows us to do better (Caswell 2007).

### 7.2 Time-Invariant Models

Armed with matrix calculus, consider the linear time-invariant model,

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t) \quad \mathbf{n}(0) = \mathbf{n}_0, \quad (7.1)$$

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where  $\mathbf{n}$  is  $s \times 1$  and  $\mathbf{A}$  is  $s \times s$ ;  $s$  the number of stages. Assume that  $\mathbf{A} = \mathbf{A}[\boldsymbol{\theta}]$  depends on a  $p \times 1$  vector of parameters  $\boldsymbol{\theta}$ , which could be entries of  $\mathbf{A}$ , lower-level parameters, or elements of the initial vector.

The sequence of matrices

$$\frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} \quad t = 1, 2, \dots \quad (7.2)$$

gives the effect of all the parameters on all the entries of  $\mathbf{n}(t)$ . From it we can calculate the sensitivities and elasticities of other dependent variables (Sect. 7.3).

We differentiate the model (7.1), obtaining

$$d\mathbf{n}(t+1) = \mathbf{A} d\mathbf{n}(t) + (d\mathbf{A}) \mathbf{n}(t), \quad (7.3)$$

and then apply the vec operator to both sides, remembering that since  $\mathbf{n}$  is a vector,  $\text{vec } \mathbf{n} = \mathbf{n}$ ,

$$d\mathbf{n}(t+1) = \mathbf{A} d\mathbf{n}(t) + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) d\text{vec } \mathbf{A}. \quad (7.4)$$

Then the first identification theorem and the chain rule, from Eqs. (2.47) and (2.18), give the sensitivity of  $\mathbf{n}(t+1)$  to the elements of  $\mathbf{A}$ ,

$$\frac{d\mathbf{n}(t+1)}{d\text{vec }^\top \mathbf{A}} = \mathbf{A} \frac{d\mathbf{n}(t)}{d\text{vec }^\top \mathbf{A}} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s). \quad (7.5)$$

The chain rule extends (7.5) to give the sensitivity to lower-level parameters,

$$\begin{aligned} \frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} &= \frac{d\mathbf{n}(t+1)}{d\text{vec }^\top \mathbf{A}} \frac{d\text{vec } \mathbf{A}}{d\boldsymbol{\theta}^\top} \\ &= \mathbf{A} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{d\text{vec } \mathbf{A}}{d\boldsymbol{\theta}^\top}. \end{aligned} \quad (7.6)$$

Equations (7.5) and (7.6) are matrix difference equations in the sensitivities of  $\mathbf{n}(t)$  to the elements of  $\text{vec } \mathbf{A}$  or of  $\boldsymbol{\theta}$ . If we know  $d\mathbf{n}(t)/d\boldsymbol{\theta}^\top$  and  $\mathbf{n}(t)$ , we can calculate  $d\mathbf{n}(t+1)/d\boldsymbol{\theta}^\top$  and  $\mathbf{n}(t+1)$  and continue this iteration to obtain the transient sensitivities at any time. If the parameters in  $\boldsymbol{\theta}$  affect the vital rates but not the initial population, the appropriate initial condition for this iteration is

$$\frac{d\mathbf{n}(0)}{d\boldsymbol{\theta}^\top} = \mathbf{0}_{s \times p}. \quad (7.7)$$

If  $\boldsymbol{\theta}$  affects only the initial population, then

$$\frac{d\mathbf{n}(0)}{d\boldsymbol{\theta}^\top} = \mathbf{I}_s \quad (7.8)$$

gives the sensitivity of transient dynamics to a change in initial conditions.

### 7.3 Sensitivity of What? Choosing Dependent Variables

The sensitivity of other dependent variables may be more interesting than that of  $\mathbf{n}(t)$ . In an early (and relatively crude) transient analysis, Caswell and Werner (1978) analyzed the transient dynamics of the plant teasel (*Dipsacus sylvestris*) in terms of rosette area at time  $t$  (which might affect resistance to invasion by later successional species) and cumulative seed production up to time  $t$  (which might affect colonization of new sites). For a weedy species like teasel, either of these dependent variables might be more relevant than the asymptotic growth rate.

Here are some other biologically more interesting dependent variables. They are easy to calculate from  $d\mathbf{n}(t)/d\boldsymbol{\theta}^\top$ .

1. Population density, as measured by a weighted sum of stage densities. Let  $\mathbf{c} \geq 0$  be a weight vector. Then population density is  $N(t) = \mathbf{c}^\top \mathbf{n}(t)$ . This includes total density ( $\mathbf{c} = \mathbf{1}_s$ , a vector of ones), the density of a subset of stages ( $c_i = 1$  for stages to be counted;  $c_i = 0$  otherwise), biomass ( $c_i$  is the biomass of stage  $i$ ), basal area, metabolic rate, etc. The sensitivity of  $N(t)$  is

$$\frac{dN(t)}{d\boldsymbol{\theta}^\top} = \mathbf{c}^\top \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top}. \quad (7.9)$$

2. Ratios measuring the relative abundances of different stages:

$$R(t) = \frac{\mathbf{a}^\top \mathbf{n}(t)}{\mathbf{b}^\top \mathbf{n}(t)}. \quad (7.10)$$

where  $\mathbf{a}$  and  $\mathbf{b}$  are weight vectors. Examples include the dependency ratio (in human demography, the ratio of the individuals below 15 or above 65 to those between 15 and 65), the sex ratio in a two-sex model, and the ratio of juveniles to adults, which is important in wildlife management (Williams et al. 2002; Skalski et al. 2005). The sensitivity of  $R(t)$  is

$$\frac{dR(t)}{d\boldsymbol{\theta}^\top} = \left( \frac{\mathbf{b}^\top \mathbf{n}(t) \mathbf{a}^\top - \mathbf{a}^\top \mathbf{n}(t) \mathbf{b}^\top}{(\mathbf{b}^\top \mathbf{n}(t))^2} \right) \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top}. \quad (7.11)$$

3. Cumulative density up to a specified time,

$$C(t) = \sum_{i=0}^t \mathbf{c}^\top \mathbf{n}(i), \quad (7.12)$$

the sensitivity of which is

$$\frac{dC(t)}{d\boldsymbol{\theta}^\top} = \mathbf{c}^\top \sum_{i=0}^t \frac{d\mathbf{n}(i)}{d\boldsymbol{\theta}^\top}. \quad (7.13)$$

4. Average density over an interval,

$$\bar{N}(t_1, t_2) = \frac{1}{t_2 - t_1} \sum_{i=t_1}^{t_2} N(i), \quad (7.14)$$

the sensitivity of which is

$$\frac{d\bar{N}(t_1, t_2)}{d\boldsymbol{\theta}^\top} = \frac{1}{t_2 - t_1} \sum_{i=t_1}^{t_2} \mathbf{c}^\top \frac{d\mathbf{n}(i)}{d\boldsymbol{\theta}^\top}. \quad (7.15)$$

5. Maximum (or minimum) density over an interval,

$$M(t_1, t_2) = \max_{t_1 \leq i \leq t_2} N(i). \quad (7.16)$$

Let  $\tilde{t}$  be the time such that  $M(t_1, t_2) = N(\tilde{t})$ . Then, except in the unlikely event of ties,

$$\frac{dM(t_1, t_2)}{d\boldsymbol{\theta}^\top} = \mathbf{c}^\top \frac{d\mathbf{n}(\tilde{t})}{d\boldsymbol{\theta}^\top} \quad (7.17)$$

with a similar expression for the minimum.

6. Variance in density over an interval  $t_1 \leq t \leq t_2$ ,

$$V(t_1, t_2) = \frac{1}{t_2 - t_1} \sum_{i=t_1}^{t_2} N^2(i) - [\bar{N}(t_1, t_2)]^2. \quad (7.18)$$

The sensitivity of  $V$  is

$$\frac{dV(t_1, t_2)}{d\boldsymbol{\theta}^\top} = \frac{2}{t_2 - t_1} \left[ \sum_{i=t_1}^{t_2} N(i) \frac{dN(i)}{d\boldsymbol{\theta}^\top} - \bar{N}(t_1, t_2) \sum_{i=t_1}^{t_2} \frac{dN(i)}{d\boldsymbol{\theta}^\top} \right] \quad (7.19)$$

$$= \frac{2}{t_2 - t_1} \left[ \sum_{i=t_1}^{t_2} \left( N(i) - \bar{N}(t_1, t_2) \right) \frac{dN(i)}{d\boldsymbol{\theta}^\top} \right]. \quad (7.20)$$

7. The transient population growth rate at time  $t$ ,

$$r(t) = \log \frac{N(t+1)}{N(t)}. \quad (7.21)$$

The sensitivity of  $r$  is

$$\frac{dr(t)}{d\boldsymbol{\theta}^\top} = \frac{\mathbf{c}^\top}{N(t+1)} \frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} - \frac{\mathbf{c}^\top}{N(t)} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top}. \quad (7.22)$$

8. Average growth rate over an interval  $t_1 \leq t \leq t_2$ ,

$$\bar{r}(t_1, t_2) = \frac{1}{t_2 - t_1} \log \frac{N(t_2)}{N(t_1)}, \quad (7.23)$$

the sensitivity of which is

$$\frac{d\bar{r}(t_1, t_2)}{d\boldsymbol{\theta}^\top} = \frac{1}{t_2 - t_1} \left( \frac{\mathbf{c}^\top}{N(t_2)} \frac{d\mathbf{n}(t_2)}{d\boldsymbol{\theta}^\top} - \frac{\mathbf{c}^\top}{N(t_1)} \frac{d\mathbf{n}(t_1)}{d\boldsymbol{\theta}^\top} \right). \quad (7.24)$$

## 7.4 Elasticity Analysis

Transient elasticities are easily calculated from the sensitivities. The elasticity of  $n_i(t)$  to  $\theta_j$  is

$$\frac{\epsilon n_i}{\epsilon \theta_j} = \frac{\theta_j}{n_i(t)} \frac{dn_i(t)}{d\theta_j}. \quad (7.25)$$

Creating a matrix of these elasticities requires multiplying column  $j$  of  $d\mathbf{n}/d\boldsymbol{\theta}^\top$  by  $\theta_j$  and dividing row  $i$  by  $n_i$ . This is just

$$\mathcal{D} [\mathbf{n}(t)]^{-1} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} \mathcal{D} [\boldsymbol{\theta}], \quad (7.26)$$

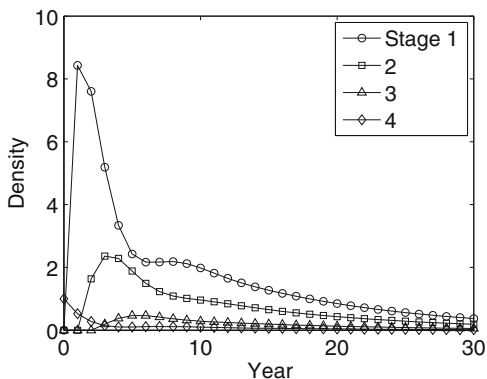
where  $\mathcal{D} [\mathbf{x}]$  is a matrix with  $\mathbf{x}$  on the diagonal and zeros elsewhere. The elasticity of any other (scalar- or vector-valued) dependent variable  $f(\mathbf{n}(t))$  is given by

$$\mathcal{D} [f(\mathbf{n}(t))]^{-1} \frac{df(\mathbf{n}(t))}{d\boldsymbol{\theta}^\top} \mathcal{D} [\boldsymbol{\theta}]. \quad (7.27)$$

**Example: A transient outbreak: elasticity to lower-level parameters** Consider a hypothetical size-classified population with

$$\mathbf{A} = \begin{pmatrix} 0.3763 & 0 & 0.8431 & 8.4312 \\ 0.1939 & 0.5421 & 0 & 0 \\ 0 & 0.1177 & 0.5240 & 0 \\ 0 & 0 & 0.1291 & 0.5254 \end{pmatrix}. \quad (7.28)$$

**Fig. 7.1** Dynamics of a transient population outbreak. The projection matrix (7.28) has  $\lambda = 0.92$ , but an initial condition of a single adult leads to a rapid outbreak that lasts for over 25 years



The asymptotic growth rate calculated as the dominant eigenvalue of  $\mathbf{A}$  is  $\lambda = 0.92$ , so the population is headed for eventual decline. However, the initial condition

$$\mathbf{n}_0 = (0 \ 0 \ 0 \ 1)^T \quad (7.29)$$

(introduction of a large adult) produces a dramatic transient outbreak (Fig. 7.1), during which total population increases by over 900% and remains above its initial value for about 25 years.<sup>1</sup>

If this was a pest its asymptotic fate (extinction) would be reassuring, but  $\lambda$  would reveal nothing about the transient outbreak. A manager might want to know how changes in the lower-level survival probabilities  $\sigma_i$ , growth probabilities  $\gamma_i$ , and fertilities  $f_i$  would affect the outbreak, where the elements of  $\mathbf{A}$  are

$$\begin{aligned} a_{ii} &= \sigma_i(1 - \gamma_i) & i = 1, \dots, 4 \\ a_{i+1,i} &= \sigma_i \gamma_i & i = 1, \dots, 3 \\ a_{1i} &= f_i & i = 3, 4. \end{aligned} \quad (7.30)$$

If the impact of the pest was related to size, the manager might measure population density with weights, say  $\mathbf{c}^T = (1 \ 2 \ 3 \ 4)$ . Two measures of damage might be the maximum of the outbreak and the cumulative population size over the entire outbreak. Finally, to put everything on a proportional basis, the manager might want to use elasticities.

<sup>1</sup>The curious reader may wish to know that  $\mathbf{A}$  was obtained by a random search for size-classified matrices with high reactivity (Neubert and Caswell 1997; Caswell and Neubert 2005; Verdy and Caswell 2008).

Define  $\theta$  as the  $9 \times 1$  vector whose entries are  $\sigma_1$ - $\sigma_4$ ,  $\gamma_1$ - $\gamma_3$ , and  $f_3$ - $f_4$ . The derivatives  $d\text{vec } \mathbf{A}/d\theta^T$  are obtained from (7.30). The sensitivity of  $\mathbf{n}(t)$  to changes in  $\theta$  is given by (7.6). Using (7.9) and (7.27) we obtain the elasticity of  $N(t)$  to  $\theta$  as

$$\frac{\epsilon N(t)}{\epsilon \theta^T} = \frac{1}{N(t)} \mathbf{c}^T \frac{d\mathbf{n}(t)}{d\theta^T} \mathcal{D}(\theta). \tag{7.31}$$

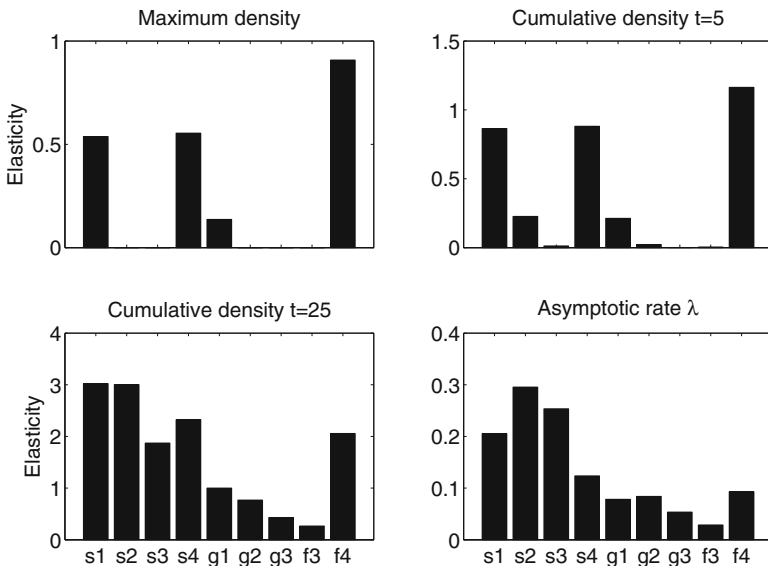
The peak of the outbreak occurs at  $t = 2$ ; thus (7.17) gives the elasticity of the peak density to  $\theta$  as

$$\frac{\epsilon N(2)}{\epsilon \theta^T} = \frac{1}{N(2)} \mathbf{c}^T \frac{d\mathbf{n}(2)}{d\theta^T} \mathcal{D}(\theta). \tag{7.32}$$

The cumulative density up to time  $t$  is given by (7.12) and the sensitivity by (7.13), so the elasticity is

$$\frac{1}{\mathbf{c}^T \sum_0^t \mathbf{n}(t)} \mathbf{c}^T \sum_{i=0}^t \frac{d\mathbf{n}(i)}{d\theta^T} \mathcal{D}(\theta). \tag{7.33}$$

Results are shown in Fig. 7.2. The elasticities of the maximum outbreak density are very different from those of  $\lambda$ . The elasticity of the cumulative density over the first 5 years has a similar pattern, also very different from that of  $\lambda$ . However, by the end of the outbreak (25 years) the elasticity of cumulative density is quite similar to that



**Fig. 7.2** The elasticities of the maximum population density, of the cumulative densities up to  $t = 5$  and  $t = 25$ , and of  $\lambda$  to the lower-level demographic parameters, for the outbreak shown in Fig. 7.1

of  $\lambda$ , so management over this time scale could reasonably rely on the elasticity of  $\lambda$  to compare control tactics. Intermediate steps and MATLAB code are found in an appendix to Caswell (2007). ■

## 7.5 Sensitivity of Time-Varying Models

Now consider the time-varying model

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t) \quad \mathbf{n}(0) = \mathbf{n}_0, \quad (7.34)$$

where  $\mathbf{A}_t, t = 1, \dots, T$  is a specified sequence of matrices.

Take the differential of both sides of (7.34)

$$d\mathbf{n}(t+1) = \mathbf{A}_t d\mathbf{n}(t) + (d\mathbf{A}_t) \mathbf{n}(t), \quad (7.35)$$

and apply the vec operator to obtain

$$d\mathbf{n}(t+1) = \mathbf{A}_t d\mathbf{n}(t) + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) (d\text{vec } \mathbf{A}_t). \quad (7.36)$$

Not only the transient behavior of the population, but also the parameter vector  $\boldsymbol{\theta}$ , the matrix  $\mathbf{A}_t$ , and the perturbation applied to  $\boldsymbol{\theta}$  may change over time. The sensitivity analysis must reflect both types of variation. So, let us treat  $\mathbf{A}_t$  as a function of  $\boldsymbol{\theta}(t)$ , and consider a perturbation of  $\boldsymbol{\theta}$  at some time  $u$ . Applying the chain rule to (7.36), we obtain

$$\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top(u)} = \mathbf{A}_t \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top(u)} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top(u)} \quad (7.37)$$

which has the same form as (7.6) except that the matrix and the matrix derivative vary over time.

Some useful simplifications follow from this formulation.

1. Perturbation of matrix elements. If  $\boldsymbol{\theta}(t)$  consists of the elements of  $\text{vec } \mathbf{A}_t$ , then

$$\frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top(t)} = \mathbf{I}_{s^2} \quad (7.38)$$

and can be eliminated from the expressions where it appears.

2. No time travel. Suppose that  $\boldsymbol{\theta}(t)$  is perturbed at some time  $t = u$ . Then

$$\frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top(u)} = \mathbf{0}_{s^2 \times p} \quad \text{for } t < u \quad (7.39)$$

However, the effects of the perturbation continue after  $t = u$ , so that  $d\mathbf{n}(t)/d\boldsymbol{\theta}^\top(u)$  will generally be non-zero for  $t > u$ .



3. Perturbations at every time. A permanent modification of the parameters can be considered a perturbation of  $\boldsymbol{\theta}(t)$  for every time  $t = 0, 1, \dots$ , so that

$$\boldsymbol{\theta}(t) \longrightarrow \boldsymbol{\theta}(t) + d\boldsymbol{\theta}. \quad (7.40)$$

The sensitivity of the population vector is then

$$\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} = \mathbf{A}_t \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top} \quad (7.41)$$

4. Perturbation over a range of times. One might be interested in perturbation over some time period  $T_1 \leq t \leq T_2$ . The effect of such a perturbation on transient dynamics is

$$\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top(u)} = \mathbf{A}_t \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top(u)} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) J(t) \frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top(u)} \quad (7.42)$$

where  $J(t)$  is an indicator variable

$$J(t) = \begin{cases} 1 & T_1 \leq t \leq T_2 \\ 0 & \text{otherwise} \end{cases} \quad (7.43)$$

These calculations have been extended to apply to population projections (Caswell and Sanchez Gassen 2015; Sanchez Gassen and Caswell 2018); see Sect. 7.8 below.

## 7.6 Sensitivity of Subsidized Populations

An interesting special case of time-varying models is that of subsidized populations (e.g., Pascual and Caswell 1991), which receive an input of individuals<sup>2</sup>

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t) + \mathbf{b}(t). \quad (7.44)$$

The subsidy vector  $\mathbf{b}(t)$  might represent immigration, or the introduction of individual animals from a captive release program, or dispersal of the larvae of marine invertebrates or the seeds of plants. If  $\mathbf{b}(t) < 0$ , then it could represent the removal or harvest of individuals from the population (e.g., Hauser et al. 2006).<sup>3</sup>

Differentiating gives:

$$\frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} = \mathbf{A}_t \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{d\text{vec } \mathbf{A}_t}{d\boldsymbol{\theta}^\top} + \frac{d\mathbf{b}(t)}{d\boldsymbol{\theta}^\top}. \quad (7.45)$$

<sup>2</sup>See Chap. 10 and Caswell (2008) for analysis of the equilibria of both linear and nonlinear versions of this equation, with applications to organizational dynamics and marine invertebrates.

<sup>3</sup>This type of harvest is unstable in the long run, but we are dealing here with transient dynamics.

If  $\theta$  affects only the vital rates and not the subsidy process, then  $d\mathbf{n}(t)/\theta^T$  reduces to (7.37), and subsidy affects the sensitivity only through its effect on  $(\mathbf{n}^T(t) \otimes \mathbf{I}_s)$ . On the other hand, setting  $\theta = \mathbf{b}$  gives the effect of changes in the subsidy process:

$$\frac{d\mathbf{n}(t+1)}{d\mathbf{b}^T} = \mathbf{A}_t \frac{d\mathbf{n}(t)}{d\mathbf{b}^T} + \mathbf{I}_s. \quad (7.46)$$

**Example: A subsidized model for the reintroduction of the Griffon vulture**

The griffon vulture (*Gyps fulvus*) was once widely distributed in Europe, but has been eliminated from many areas, due primarily to poisoning and shooting. A reintroduction program has re-established a population in the Massif Central of southern France; Sarrazin and Legendre (2000) have analyzed this program. Reintroduction programs are increasingly important in conservation biology (Sarrazin and Barbault 1996; Snyder and Snyder 2000), and will become an important application of subsidized models. Transient dynamics are naturally critical for evaluating reintroduction programs, because the programs are of finite duration and are evaluated by short-term measures of success at, or shortly after, their conclusion.

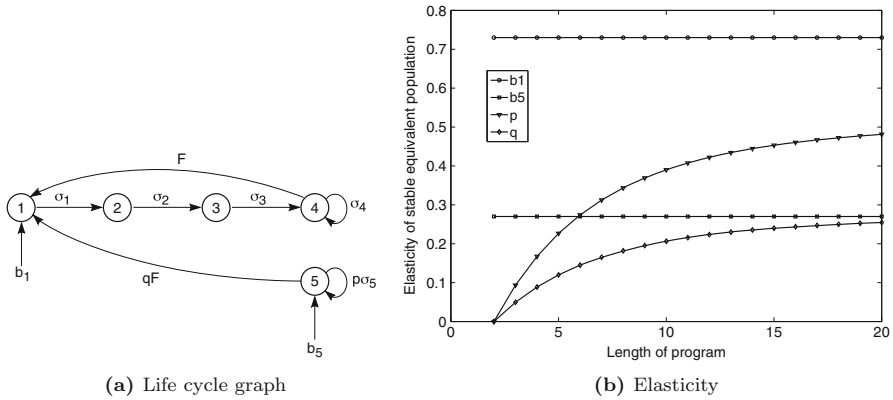
In the case of the griffon vulture, birds can be introduced as juveniles or adults. Adults introduced from captivity have lower fertility and lower survival than wild adults. Here I use a simplification of the Sarrazin-Legendre model to show how transient sensitivity analysis could be used. The life cycle contains four age classes and a stage representing captive-reared adults (Fig. 7.3a). The survival of released adults is a fraction  $p$  of that of wild adults, and their fertility a fraction  $q$  of that of the wild adults. I assume these costs persist indefinitely; Sarrazin and Legendre (2000) explore both short- and long-term costs. Suppose that a manager is interested in the effects of the annual number  $b_1$  of juveniles released, the number  $b_5$  of adults released, and the relative survival  $p$  and relative fertility  $q$  of captive-reared adults.

One measure of success will be the population size at the end of the introduction program. The best such population, in terms of future population size, would be one with the highest total reproductive value,  $N = \mathbf{v}^T \mathbf{n}$  (also called the stable equivalent population; see Chapters 8–9 of Keyfitz and Caswell 2005). The elasticity of stable equivalent population size<sup>4</sup> is

$$\frac{\epsilon N}{\epsilon \theta^T} = \frac{1}{\mathbf{v}^T \mathbf{n}(t)} \mathbf{v}^T \frac{d\mathbf{n}(t)}{d\theta^T} \mathcal{D}(\theta) \quad t = 1, \dots, T \quad (7.47)$$

where  $\mathbf{v}$  is the reproductive value vector from  $\mathbf{A}$  and  $\theta^T = (b_1 \ b_5 \ p \ q)$ .

<sup>4</sup>The parameters under investigation here do not affect the reproductive value vector  $\mathbf{v}$ . To analyze the sensitivity of stable equivalent population to, say,  $\sigma_i$ , would require the derivative of  $\mathbf{v}$  as well; this is presented in Chap. 10.



**Fig. 7.3** (a) The life cycle graph and (b) the transient elasticity of stable equivalent population size  $N(t) = \mathbf{v}^T \mathbf{n}(t)$  to changes in juvenile introductions ( $b_1$ ), adult introductions ( $b_5$ ), adult survival costs ( $p$ ), and adult fertility costs ( $q$ ) for the Griffon vulture. Parameter values from Sarrazin and Legendre (2000);  $\sigma_j = 0.86$ ,  $\sigma_a = 0.98$ ,  $f = 0.33$ ,  $p = 0.75$ ,  $q = 0.51$

Using parameter values in Sarrazin and Legendre (2000) and setting  $b_1 = b_5$  (i.e., evaluating the value of juveniles and adults from a situation where they are introduced in equal numbers) gives the result in Fig. 7.3b, for an introduction program duration of up to 20 years.

It is always better to increase the number of juveniles relative to the number of adults introduced. The benefits of reducing survival and fertility costs (i.e., increasing  $p$  or  $q$ ) increases with the duration of the program, as they have longer times available to operate. Reductions in the survival cost would have more impact than reductions in the fertility costs. These results are strongly influenced by the fact that the reproductive value of captive-reared adults is lower than that of newly fledged or released juveniles, which is reflected in the high elasticity of  $N(t)$  to juvenile releases. ■

## 7.7 Sensitivity of Nonlinear Models

In density- or frequency-dependent models, the vital rates  $\mathbf{A}$  depend on the parameters  $\boldsymbol{\theta}$  and current population density  $\mathbf{n}(t)$ :

$$\mathbf{n}(t + 1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)] \mathbf{n}(t). \tag{7.48}$$

Changes in  $\boldsymbol{\theta}$  affect dynamics directly, through  $\mathbf{A}$ , and indirectly, through  $\mathbf{n}(t)$ . The transient sensitivity of  $\mathbf{n}(t)$  to parameter changes must include both effects.

Differentiating both sides of (7.48) and applying the vec operator gives the familiar differential expression

$$d\mathbf{n}(t + 1) = \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]d\mathbf{n}(t) + (\mathbf{n}^T(t) \otimes \mathbf{I}_s) d\text{vec } \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]. \tag{7.49}$$

But now, unlike in the linear case,  $d\text{vec } \mathbf{A}$  includes both direct effects through  $\boldsymbol{\theta}$  and indirect effects through  $\mathbf{n}$ , so the total differential is

$$d\text{vec } \mathbf{A} = \frac{\partial \text{vec } \mathbf{A}}{\partial \boldsymbol{\theta}^\top} d\boldsymbol{\theta} + \frac{\partial \text{vec } \mathbf{A}}{\partial \mathbf{n}^\top} \frac{\partial \mathbf{n}(t)}{\partial \boldsymbol{\theta}^\top} d\boldsymbol{\theta}. \quad (7.50)$$

Substituting (7.50) into (7.49) gives

$$\begin{aligned} \frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} &= \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)] \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} \\ &\quad + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{\partial \text{vec } \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]}{\partial \boldsymbol{\theta}^\top} \\ &\quad + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{\partial \text{vec } \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]}{\partial \mathbf{n}^\top(t)} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top}. \end{aligned} \quad (7.51)$$

The first two terms are familiar from the density-independent case; the third term accounts for the effects of  $\boldsymbol{\theta}$  on  $\mathbf{A}$  through its effects on  $\mathbf{n}(t)$ . Rearranging terms gives the transient sensitivity,

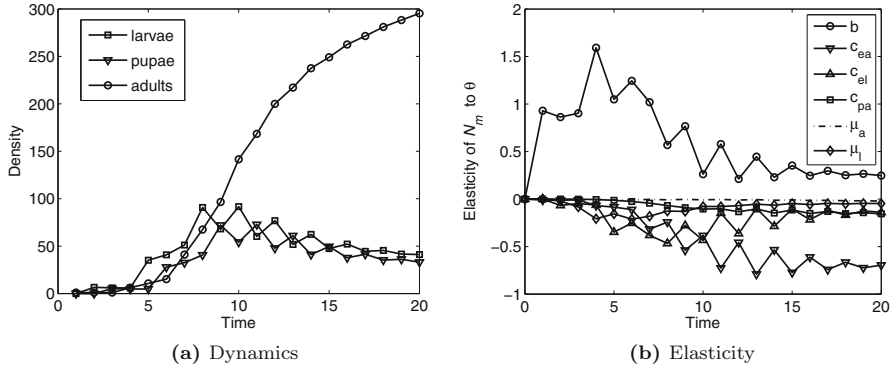
$$\begin{aligned} \frac{d\mathbf{n}(t+1)}{d\boldsymbol{\theta}^\top} &= \left\{ \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)] + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{\partial \text{vec } \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]}{\partial \mathbf{n}^\top(t)} \right\} \frac{d\mathbf{n}(t)}{d\boldsymbol{\theta}^\top} \\ &\quad + (\mathbf{n}^\top(t) \otimes \mathbf{I}_s) \frac{\partial \text{vec } \mathbf{A}[\boldsymbol{\theta}, \mathbf{n}(t)]}{\partial \boldsymbol{\theta}^\top}. \end{aligned} \quad (7.52)$$

**Example: Transient sensitivity of *Tribolium*** Flour beetles of the genus *Tribolium* have been used for a series of models of, and experiments on, nonlinear dynamics, reviewed by Cushing et al. (2003). *Tribolium* lives in stored flour. Adults and larvae cannibalize eggs, and adults cannibalize pupae; these interactions provide the density-dependence, and are captured in a three-stage (larvae, pupae, and adults) model, with

$$\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}] = \begin{pmatrix} 0 & 0 & b \exp(-c_{el}n_1 - c_{ea}n_3) \\ 1 - \mu_l & 0 & 0 \\ 0 & \exp(-c_{pa})n_3 & 1 - \mu_a \end{pmatrix} \quad (7.53)$$

where  $b$  is the clutch size,  $c_{ea}$ ,  $c_{el}$ , and  $c_{pa}$  are cannibalism rates (of eggs by adults, eggs by larvae, and pupae by adults), and  $\mu_l$  and  $\mu_a$  are larval and adult mortalities. Parameter values from experiments reported by Costantino et al. (1997) give the transient dynamics in Fig. 7.4, following introduction of a single adult.

The sensitivity of this transient behavior requires the derivatives of  $\mathbf{A}[\boldsymbol{\theta}, \mathbf{n}]$  to the parameters and to the densities. Substituting these derivatives into (7.52) gives the transient sensitivities by a simple iteration. The derivative matrices are given in an appendix to Caswell (2007).



**Fig. 7.4** (a) The transient dynamics of the *Tribolium* model following introduction of a single adult. Parameters from Costantino et al. (1997). (b) The transient elasticity of the metabolic population size  $N_m(t)$  to each of the parameters of the *Tribolium* model, for the first 20 time steps following the introduction of a single adult

*Tribolium* is a pest. The damage it causes might, I suppose, be related to its consumption, which might be measured by the metabolic rate. Emekci et al. (2001) estimated the per capita metabolic rate of larvae, pupae, and adults. Using their results, we define the metabolic population size as  $N_m(t) = \mathbf{c}^T \mathbf{n}(t)$  where  $\mathbf{c}^T = (9 \ 1 \ 4.5) \mu\text{l CO}_2 \text{ h}^{-1}$ . The elasticities of  $N_m(t)$  to the parameters are

$$\frac{\epsilon N_m}{\epsilon \theta^T} = \frac{1}{N_m(t)} \mathbf{c}^T \frac{d\mathbf{n}(t)}{d\theta^T} \mathcal{D}(\theta). \tag{7.54}$$

for  $t = 1, \dots, 20$ .

The results are shown in Fig. 7.4. For the first 5 or so iterations,  $N_m$  is more elastic to the clutch size than to the cannibalism or mortality rates. After that, the impact of  $b$  declines and the impact (negative) of the cannibalism coefficients increases. Beyond 10 time steps,  $N_m$  is affected primarily by  $b$  (positively) and  $c_{ea}$  (negatively). Changes in mortality ( $\mu_a$  and  $\mu_l$ ) have only small effects. Such changes in the relative impact of the parameters over short periods of time are typical of transient sensitivities. Interestingly, the elasticities of total population size  $N_{\text{tot}} = \sum n_i$  (not shown) show a similar pattern, but lack the period-2 fluctuation evident in Fig. 7.4. This reflects the interaction of the weighting pattern (much more uneven in the calculation of  $N_m$  than  $N_{\text{tot}}$ ) and transient fluctuations in the stage distribution. Asymptotic sensitivity calculations are unaffected by such differences.

The parameter values used here lead to a stable equilibrium, but the transient calculations apply equally to other types of dynamics. ■

## 7.8 Sensitivity of Population Projections

The most common transient analyses of populations appear in the population projections provided by local, national, and international offices. These projections are usually carried out by the cohort component method, which uses mortality, fertility, and migration to describe the dynamics of each age $\times$ sex combination. The calculations are transient because they begin with the current, rather than an asymptotic, age-sex distribution and are carried out over a short time horizon (usually a few decades). In the first issue of the first volume of the then-new journal *Demography*, Nathan Keyfitz described the “population projection as a matrix operator” (Keyfitz 1964). He showed that population projections using the cohort component method could be written as matrix population models, and emphasized the value in doing so to focus attention on the mathematical structure of the projection, inviting deeper analyses of its properties with more powerful mathematical tools. Considering projections as matrix operators allows the use of matrix calculus methods to develop a thorough perturbation analysis of population projections (Caswell and Sanchez Gassen 2015; Sanchez Gassen and Caswell 2018).

To present the basics of projection sensitivity analysis, we begin with a simple one-sex model, but we focus most of our attention on a two-sex model that includes separate rates for males and females.

The single-sex projection can be written as

$$\mathbf{n}(t + 1) = \mathbf{A}(t)\mathbf{n}(t) + \mathbf{b}(t) \quad \mathbf{n}(0) = \mathbf{n}_0 \quad (7.55)$$

where  $\mathbf{n}(t)$  is a vector whose entries are the numbers of individuals in each age class or stage at time  $t$ ,  $\mathbf{A}(t)$  is a projection matrix incorporating the vital rates at time  $t$ , and  $\mathbf{b}(t)$  is a vector giving the number of immigrants in each age class or stage at time  $t$ . The projection begins with a specified initial condition, denoted  $\mathbf{n}_0$ , and is carried out until some target time  $T$ .

To develop a two-sex projection, we define population vectors  $\mathbf{n}_f$  and  $\mathbf{n}_m$ , and projection matrices  $\mathbf{A}_f$  and  $\mathbf{A}_m$ , for females and males, respectively. We assume that reproduction is female dominant,<sup>5</sup> so all fertility is attributed to females. We decompose the projection matrices for females and males into

$$\mathbf{A}_f(t) = \mathbf{U}_f(t) + \phi\mathbf{F}(t) \quad (7.56)$$

$$\mathbf{A}_m(t) = \mathbf{U}_m(t) \quad (7.57)$$

where  $\mathbf{U}$  describes transitions and survival of extant individuals and  $\mathbf{F}$  describes the production of new individuals by reproduction.

---

<sup>5</sup>Two-sex models that do not assume dominance by one sex have been used to project animal populations, but not, as far as I know, human populations (e.g., Jenouvrier et al. 2009, 2010, 2012).

In an age-classified model,  $\mathbf{F}$  will have effective fertilities (including infant and maternal survival as appropriate) on the first row and zeros elsewhere. A proportion  $\phi$  of the offspring are female. This model attributes reproduction to females; hence there is no need to create separate fertility matrices for reproduction by males and females.

The male component of the population is projected by the survival matrix  $\mathbf{U}_m$ ; the input of new individuals comes from the female population. The projection model becomes

$$\mathbf{n}_f(t+1) = \left[ \mathbf{U}_f(t) + \phi \mathbf{F}(t) \right] \mathbf{n}_f(t) + \mathbf{b}_f(t) \quad (7.58)$$

$$\mathbf{n}_m(t+1) = \mathbf{U}_m(t) \mathbf{n}_m(t) + (1 - \phi) \mathbf{F}(t) \mathbf{n}_f(t) + \mathbf{b}_m(t) \quad (7.59)$$

The sensitivity of the two-sex projection is given by the two derivatives,

$$\frac{d\mathbf{n}_f(t)}{d\boldsymbol{\theta}^\top(u)} \quad \text{and} \quad \frac{d\mathbf{n}_m(t)}{d\boldsymbol{\theta}^\top(u)} \quad t, u = 0, \dots, T.$$

These sensitivities are obtained from dynamic expressions, for the female population

$$\begin{aligned} \underbrace{\frac{d\mathbf{n}_f(t+1)}{d\boldsymbol{\theta}^\top(u)}}_{\text{sensitivity at } t+1} &= \underbrace{\left( \mathbf{U}_f(t) + \phi \mathbf{F}(t) \right) \frac{d\mathbf{n}_f(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{sensitivity at } t} + \underbrace{\left( \mathbf{n}_f^\top(t) \otimes \mathbf{I}_\omega \right) \left( \frac{d\text{vec } \mathbf{U}_f(t)}{d\boldsymbol{\theta}^\top(u)} + \phi \frac{d\text{vec } \mathbf{F}(t)}{d\boldsymbol{\theta}^\top(u)} \right)}_{\text{effects via female transitions and fertility}} \\ &+ \underbrace{\frac{d\mathbf{b}_f(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{effects via immigration}} \end{aligned} \quad (7.60)$$

and the male population

$$\begin{aligned} \underbrace{\frac{d\mathbf{n}_m(t+1)}{d\boldsymbol{\theta}^\top(u)}}_{\text{sensitivity at } t+1} &= \underbrace{\mathbf{U}_m(t) \frac{d\mathbf{n}_m(t)}{d\boldsymbol{\theta}^\top(u)} + (1 - \phi) \mathbf{F}(t) \frac{d\mathbf{n}_f(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{sensitivities at } t} + \underbrace{\left( \mathbf{n}_m^\top(t) \otimes \mathbf{I}_\omega \right) \frac{d\text{vec } \mathbf{U}_m(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{effects via male transitions}} \\ &+ \underbrace{(1 - \phi) \left( \mathbf{n}_f^\top(t) \otimes \mathbf{I}_\omega \right) \frac{d\text{vec } \mathbf{F}(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{effects via female fertility}} + \underbrace{\frac{d\mathbf{b}_m(t)}{d\boldsymbol{\theta}^\top(u)}}_{\text{effects via immigration}} \end{aligned} \quad (7.61)$$

Equations (7.60) and (7.61) are iterated from initial conditions

$$\frac{d\mathbf{n}_f(0)}{d\boldsymbol{\theta}^\top(u)} = \frac{d\mathbf{n}_m(0)}{d\boldsymbol{\theta}^\top(u)} = \mathbf{0}_{\omega \times p} \quad (7.62)$$

along with the iteration of equations (7.58) and (7.59) for the population vectors  $\mathbf{n}_f(t)$  and  $\mathbf{n}_m(t)$ . For complete details, see Caswell and Sanchez Gassen (2015).

The terms in (7.61) are labelled to show how the processes of transitions, fertility and migration, for males and females, combine to produce sensitivity of a transient population. As before, the sensitivity at  $t + 1$  depends on the sensitivity at time  $t$  and on the effects of the parameter vector on the transition and fertility matrices and on the immigration vector. In the next section we turn to the calculation of these derivatives.

The elasticities of  $\mathbf{n}_f(t)$  are given by

$$\frac{\epsilon \mathbf{n}_f(t)}{\epsilon \boldsymbol{\theta}^\top(u)} = \mathcal{D} \left[ \mathbf{n}_f(t) \right]^{-1} \frac{d\mathbf{n}_f(t)}{d\boldsymbol{\theta}^\top(u)} \mathcal{D} \left[ \boldsymbol{\theta}(u) \right] \quad (7.63)$$

with a similar expression for  $\mathbf{n}_m$ .

Caswell and Sanchez Gassen (2015) present a detailed analysis of a projection for the population of Spain, published by the Instituto Nacional de Estadística (INE), for the years 2012–2052. They calculated the sensitivity and elasticity of total population, male and female population, the school age population (6–16 years), the part of the population expected to suffer from dementia, and the dependency and support ratios. All these outcomes are calculated from the basic projection using the methods in Sect. 7.3. In a more extensive comparison, Sanchez Gassen and Caswell (2018) have applied the approach to the EuroPop2013 projections for the 28 member states of the European Union, plus Iceland, Norway, and Sweden, for the years 2013–2080.

## 7.9 Discussion

In addition to their obvious role in population projections, transient effects are critically important in studies of climate change and other short term management issues (Ezard et al. 2010). A recent study found that simulations of invasive species were strongly influenced by transient effects (Muthukrishnan et al. 2018). Matrix calculus makes transient sensitivity analysis straightforward and applicable to a wide range of models and perturbations. The approach calculates sensitivities and elasticities as a dynamic system, iterated in parallel with the dynamics of the transient solution itself.

This dynamic approach reveals the fundamental structure underlying the sensitivity calculation. The results bear a striking family resemblance, from the linear, time-invariant case (7.6), to the time-varying case (7.41), the case of subsidized populations (7.45), the nonlinear case (7.52), and the time-varying, two-sex, subsidized model that forms the basis for the cohort component method of population projection in equations (7.61) and (7.60).

The examples here sound like stories—*suppose that* someone (e.g., a manager) is interested in some aspect of the population (e.g., its total size, or variance, or



average growth,...) over some time interval. Or *suppose* that mortality, fertility, and immigration develop in the following way. This emphasizes the flexibility of this approach, and also the importance about thinking clearly about the dependent variables and time scales of interest. The list of dependent variables in Sect. 7.3 can no doubt be extended. It may be repeating the obvious, but transient sensitivity analysis depends on initial conditions. Each of the examples had to choose an initial condition and argue for its relevance.

Section 10.2.6 in Chap. 10 briefly considers the sensitivity analysis of equilibria to continuous-time systems. Richard et al. (2015) have developed a very general sensitivity analysis of transient dynamics in continuous systems (both linear and nonlinear). They point out and nicely demonstrate the parallels between continuous-time models and the discrete-time models considered here, the link being the creation of a dynamic model for the sensitivities that is solved along with the dynamics of the system itself.

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