

8

Projecting Populations

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Summary

Population dynamics models allow us to predict, explain, or remedy population trends given the biology of the species and the characteristics of its environment. In the approach proposed here, the key concept is the life cycle graph, a representation of the life history of a given species, parameterized by the demographic parameters, the fecundity and survival rates. I describe how deterministic systems in discrete time are built from the life cycle graph, and how demographic descriptors (growth rate, generation time, sensitivities) can be computed. Regulation by population density and the spatial component (metapopulation) are introduced. Stochastic models are then constructed from the deterministic models, to account for fluctuations in the environment and for demographic stochasticity, that is, random population drift. Though the chapter contains many mathematical formulas, it mostly relies on biological intuition.

8.1 Introduction

The aim of this chapter is to provide a broad overview of population dynamics methods that are useful for practical applications. These methods rely on solid theoretical grounds, and this necessitates the use of mathematical concepts and equations. The reader should not be put off by the presence of mathematical formulas, and can skip some of them (in particular Boxes 8.3–8.5) and rely on the intuitive meaning given in the text. Experience shows that biological intuition is enough to develop pertinent population models without being mathematically inclined. I however believe that mathematical formulas remain the most concise and universal way of transmitting information.

The key concept of the chapter is the *life cycle graph*, introduced in Section 8.2. It is a simple concept which has far-reaching consequences. Once mastered, it goes well along with biological sense, but its construction and interpretation are crucial first steps. Then, matrix algebra and the theory of stochastic processes are convenient tools to analyze the properties of a given life cycle.

Population dynamics is the study of population trajectories or variation in population sizes over time, which is necessary for predicting, explaining, or managing population trends. In the framework of population dynamics, a *population* is defined as a set of individuals of the same genotype, living in the same environment. Accordingly,

all individuals in a population are considered identical to an average individual. The average individual is described by the life cycle graph, a schematic description of the stages traversed by an organism during its life. The life cycle graph, whose parameters are determined from individual data (survival rates, fecundities, life span), is constructed according to the biology of the species and the question of interest.

From the life cycle graph, *matrix population models* and variants thereof are built, allowing to project the population in *discrete time* $t = 0, 1, 2, \dots$ Discrete time is well suited because many organisms reproduce seasonally. Also, demographic parameters, survival and fecundity rates, are measured in the field or in the laboratory at regular dates, in relation with the periodical schedule of the species.

Matrix population models provide pertinent demographic descriptors: growth rate, generation time, and the most sensitive parameters, those that contribute most to the dynamics. These models can also account for environmental characteristics such as limitation of resources leading to population regulation or environmental fluctuations, as well as other specific features such as spatial structure or harvesting, thereby leading to demographic predictors like the probability of extinction. Matrix models form a multipurpose toolbox for the management and conservation of species, and can also address evolutionary issues.

8.2 The Life Cycle Graph

8.2.1 Description

All organisms traverse different stages during their life, typically immature stages where they develop followed by mature stages where they reproduce. This scheme is represented by the life cycle graph, a directed graph whose *nodes* describe the stages, and whose *arcs* describe transitions from one stage to the next. Demographic parameter values (vital rates) are associated with the *transitions*, representing the contribution of a stage to the next (Figure 8.1). The life cycle graph can be seen as a simplification and quantification of the developmental process and of the contribution of one generation to the next. The same duration is associated with each transition. It will be the time step of the discrete time dynamical system built from the life cycle graph.

To project a population, first construct the life cycle graph of the species. All population dynamics models are based, explicitly or not, on such a representation. The life cycle graph accounts for the biology of the species, depends on the available individual data, and is constructed to address the question of interest.

The life cycle is in general assumed to be *female-based*: the population is considered to be constituted of females only. It means that there are always enough males to fertilize the females, and that the male life cycle does not differ from the female life cycle. These two assumptions are not always met, and will be relaxed when considering *two-sex models* (Section 8.8.2).

Figure 8.1b represents the life cycle graph of a short-lived species such as a small songbird or a small lizard. This example will be used throughout the text and referred as the *passerine model* (Legendre et al. 1999). In this example, the population census occurs shortly before reproduction (*prebreeding census*). There are two age classes: individuals aged one year (subadults), and individuals aged two years or more (adults). Subadults reproduce with fecundity f_1 and become adults with subadult survival rate s_1 . Adults reproduce with fecundity f_2 and stay in the adult class according to the survival rate s_2 , as expressed by the self-loop in the adult stage. Because of the prebreeding census, a newborn will be censused the following year, when it is (almost) one year old: it survives with juvenile survival rate s_0 before entering the one-year-old age class. This is why the juvenile survival rate s_0 multiplies the fecundities in the reproductive transitions. As the life cycle is female-based, only females giving birth to females are considered: the primary female sex ratio σ (the proportion of females at birth) multiplies the fecundities. In many species the primary sex ratio is balanced: $\sigma = 0.5$.

In a *postbreeding census*, the population census occurs shortly after reproduction, and the first stage consists of

zero-year-old individuals. In the passerine model, there are now three age classes instead of two. The age-0 individuals are descendants of the juveniles, subadults, and adults censused the previous year, which survived (for almost one year) at rates s_0 , s_1 , and s_2 respectively (Figure 8.1c). To summarize, in the prebreeding census the juvenile survival rate s_0 multiplies the fecundities, whereas in the postbreeding census there is a supplementary stage (age-0 individuals), and age-specific survival rates multiply the fecundities (Figure 8.1b). Both representations lead to the same demographic descriptors (Section 8.3.2).

8.2.2 Construction

The life cycle graph is constructed in three steps:

- 1) Determine the largest *time step* compatible with the biology of the species and the observations. Typically, the time step might be a year for birds and large mammals, a month for small mammals, or a day for insects. Recall that all arcs in the life cycle graph correspond to the same time step.
- 2) Determine the pertinent stages. For many organisms, the convenient stages are *age classes*, with the identification of the age at first reproduction. However, several organisms are better classified according to other criteria, like size. *Size classes* are often preferred for plants whose development is much more plastic than animals, because growth can be delayed until sufficient light exposure is met, and because observations are more conveniently performed in terms of size rather than age. Size-classified models (Figure 8.1f) are also used for animal species like turtles, fish, and reptiles (Morris and Doak 2002; Crouse et al. 1987). In Figure 8.1f, g_i is the probability to grow from a size class to the next.

In general, any structure can be used for the stages, provided that they are biologically relevant. In fact, life cycles are very diverse across plant and animal taxa (Jones et al. 2014). In many cases, it is convenient to incorporate in an age- or size-classified model stages that account for biological specificities or for the question of interest. For example, the life cycle of the wolf *Canis lupus* (Figure 8.1c2, Chapron et al. 2003) is not strictly age-classified. We have pups (0–6 months), juveniles (6–18 months), subadults (18–30 months), adults (30+ months), and two more stages that account for characteristics of this social species: dispersers (dispersing juveniles must wait one year before looking for a mate), and pack leaders. In stage-classified models, a same duration is still associated with each transition. However, individuals in a stage are of different ages, and individuals of the same age

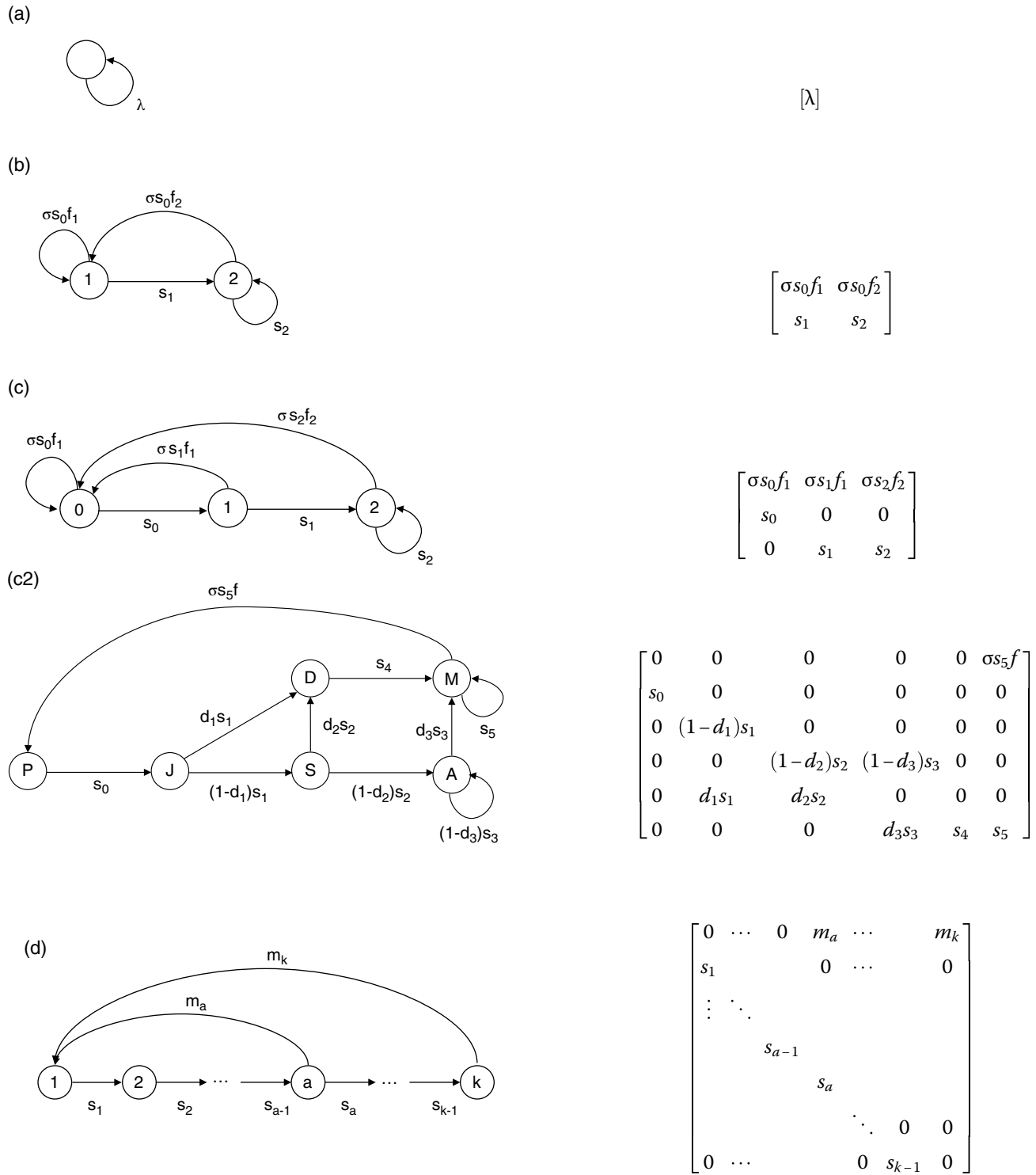
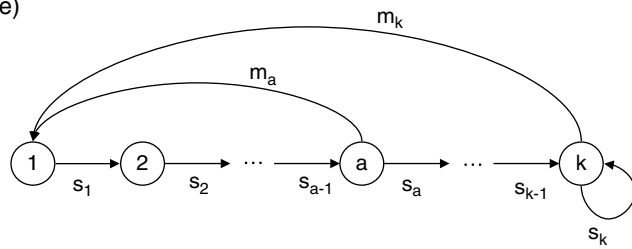


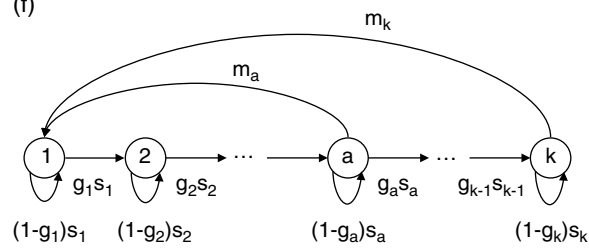
Figure 8.1 A library of life cycle graphs with corresponding population matrices. (a) Unstructured life cycle. (b) Life cycle for passerine (prebreeding census). (c) Life cycle for passerine (postbreeding census). (c2) Life cycle for the wolf *Canis lupus*. Stages: P = pups, J = juveniles, S = subadults, A = adults, D = dispersers, M = dominant. (d) Leslie age-classified life cycle (s_i survival rate, m_i fertility rate, a age at first reproduction). (e) Age-classified life cycle (Leslie model with self-loop on the last age class). (f) Size-classified life cycle (s_i survival rate, g_i probability to grow, m_i fertility rate, a age at first reproduction). (g) Age-classified life cycle with postreproductive stage (reducible matrix). (h) Semelparous life cycle (periodic matrix). (i) Life cycle with gap in reproduction (periodic matrix). (j) Life cycle with stages for immigrant pool (I) and emigrant pool (E). (k) Life cycles of two sites, A and B, connected by migrations. (l) Two-sex life cycle with underlying mating function μ . (m) Individual heterogeneity: two developmental pathways according to function J .

(e)



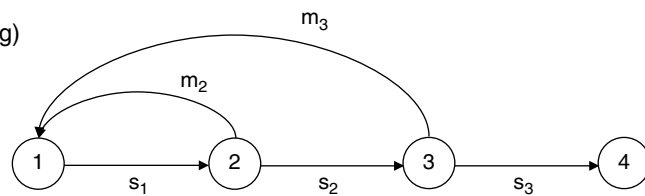
$$\begin{bmatrix} 0 & \cdots & 0 & m_a & \cdots & m_k \\ s_1 & & 0 & \cdots & & 0 \\ \vdots & \ddots & & & & \\ & & s_{a-1} & & & \\ & & & s_a & & \\ & & & & \ddots & 0 & 0 \\ 0 & \cdots & & 0 & s_{k-1} & s_k \end{bmatrix}$$

(f)



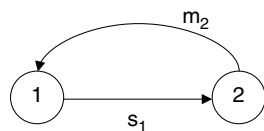
$$\begin{bmatrix} (1-g_1)s_1 & \cdots & 0 & m_a & \cdots & m_k \\ g_1s_1 & (1-g_2)s_2 & & 0 & \cdots & 0 \\ \vdots & \ddots & & & & \\ & & g_{a-1}s_{a-1} & (1-g_a)s_a & & \\ & & & g_as_a & & \\ & & & & \ddots & (1-g_{k-1})s_{k-1} & 0 \\ 0 & \cdots & & 0 & g_{k-1}s_{k-1} & (1-g_k)s_k \end{bmatrix}$$

(g)



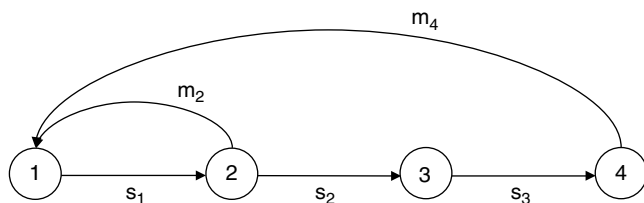
$$\begin{bmatrix} 0 & m_2 & m_3 & 0 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix}$$

(h)



$$\begin{bmatrix} 0 & m_2 \\ s_1 & 0 \end{bmatrix}$$

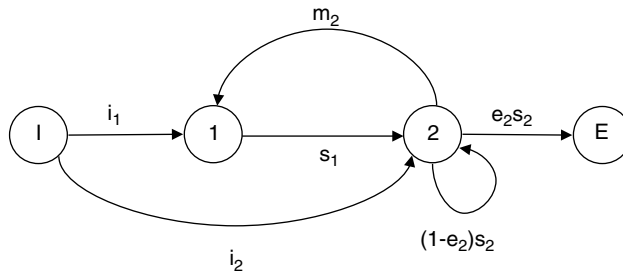
(i)



$$\begin{bmatrix} 0 & m_2 & 0 & m_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix}$$

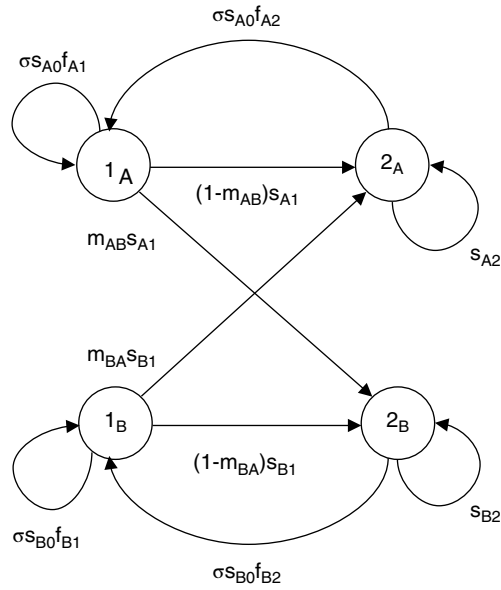
Figure 8.1 (Continued)

(j)



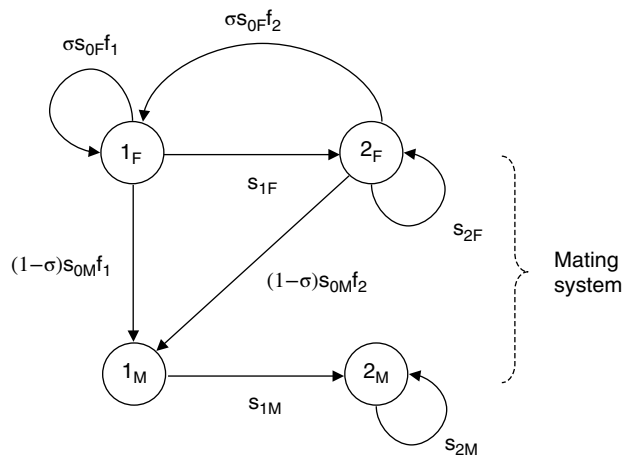
$$\begin{bmatrix} 0 & m_2 & i_1 & 0 \\ s_1 & (1-e_2)s_2 & i_2 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & e_2s_2 & 0 & 0 \end{bmatrix}$$

(k)



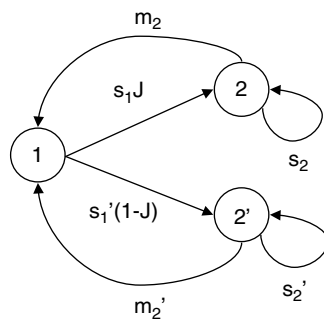
$$\begin{bmatrix} \sigma s_{A0}f_{A1} & \sigma s_{A0}f_{A2} & 0 & 0 \\ (1-m_{AB})s_{A1} & s_{A2} & m_{BA}s_{B1} & 0 \\ 0 & 0 & \sigma s_{B0}f_{B1} & \sigma s_{B0}f_{B2} \\ m_{AB}s_{A1} & 0 & (1-m_{BA})s_{B1} & s_{B2} \end{bmatrix}$$

(l)



$$\begin{bmatrix} \sigma s_{0F}f_1 \frac{\mu}{f} & \sigma s_{0F}f_2 \frac{\mu}{f} & 0 & 0 \\ s_{1F} & s_{2F} & 0 & 0 \\ (1-\sigma)s_{0M}f_1 \frac{\mu}{f} & (1-\sigma)s_{0M}f_2 \frac{\mu}{f} & 0 & 0 \\ 0 & 0 & s_{1M} & s_{2M} \end{bmatrix}$$

(m)



$$\begin{bmatrix} 0 & m_2 & m_2' \\ s_1J & s_2 & 0 \\ s_1'(1-J) & 0 & s_2' \end{bmatrix}$$

Figure 8.1 (Continued)

may be in different stages, which can make the results more difficult to intuit.

- 3) Determine the *demographic parameters* associated with the transitions of the life cycle from individual data. For wild populations, survival rates are usually estimated using known fate models (Chapter 6), or with capture-mark-recapture methods (Lebreton et al. 1992; Sandercock 2006; Chapter 7). Uninformed parameters may be left as variables that can be explored using different scenarios, or filled with guess values taken from the literature for a related species. It will be seen that some demographic parameters have little influence on population dynamics (sensitivities, Section 8.3.3), so that accurate estimation is not crucial.

8.3 Matrix Models

8.3.1 The Projection Equation

The simplest life cycle graph has a single class (Figure 8.1a). In this *unstructured model*, population size n grows by a constant multiplicative factor from one time step to the next:

$$n(t+1) = \lambda n(t). \quad (8.1)$$

The *population growth rate* (λ) describes the (average) contribution of each individual alive at time t to population size at time $t+1$. The contribution involves survival and fecundity: $\lambda = s + f$. We have *nonoverlapping generations* when, in a time step, individuals give birth to f offspring and then die ($s = 0$). In this case, a time step corresponds to a generation, and the *generation time* is $T = 1$. Otherwise, generations overlap.

Population size is given by a geometric series in Eq. (8.1), so that

$$n(t) = \lambda^t n(0), \quad (8.2)$$

where $n(0)$ is initial population size. From Eq. (8.2), we deduce that population size grows exponentially to infinity when $\lambda > 1$, and decreases exponentially to 0 when $\lambda < 1$.

Let us consider a general life cycle graph with k stages (e.g. Figure 8.1b where $k = 2$, or Figure 8.1d–f). A square matrix $\mathbf{A} = (a_{ij})$ of size $k \times k$ is associated with the life cycle graph: the entry a_{ij} of \mathbf{A} describes the contribution of an individual from stage j to stage i during a time step when there is an arc from j to i , and is 0 otherwise. Thus a non-zero entry a_{ij} of \mathbf{A} corresponds to the arc $j \rightarrow i$. Its value is the demographic parameter associated with the transition $j \rightarrow i$. Let $n_i(t)$ denote the number of individuals in stage i at time t , then summing contributions,

$$n_i(t+1) = \sum_{j=1}^k a_{ij} n_j(t). \quad (8.3)$$

Introducing the column population vector $\mathbf{n}(t) = (n_1(t), \dots, n_k(t))$, we recognize in Eq. (8.3) the product of the matrix \mathbf{A} by the vector $\mathbf{n}(t)$. Hence, the population vector is updated from a time step to the next according to

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \quad (8.4)$$

which gives

$$\mathbf{n}(t) = \mathbf{A}^t \mathbf{n}(0). \quad (8.5)$$

A convention in matrix algebra is that boldface type is used to denote matrices and vectors.

Let us describe the procedure for the passerine model. Let $n_1(t)$ be the number of one-year old individuals at time t , $n_2(t)$ the number of individuals aged two years or more at time t . Inspection of the life cycle graph (Figure 8.1b) tells us that population sizes in the stages are updated from one time step to the next according to

$$n_1(t+1) = \sigma s_0 f_1 n_1(t) + \sigma s_0 f_2 n_2(t), \quad (8.6)$$

$$n_2(t+1) = s_1 n_1(t) + s_2 n_2(t).$$

These equations can be written in matrix form:

$$\begin{bmatrix} n_1 \\ n_2 \end{bmatrix}_{t+1} = \begin{bmatrix} \sigma s_0 f_1 & \sigma s_0 f_2 \\ s_1 & s_2 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \end{bmatrix}_t. \quad (8.7)$$

For an age-classified life cycle with k stages and pre-breeding census, the associated $k \times k$ matrix is shown in Figure 8.1e, where a is age at first reproduction and it is assumed that reproductive individuals have constant survival s_k and constant fecundity f_k from age k . When all individuals die at age k , $s_k = 0$, we obtain the Leslie matrix (Figure 8.1d).

The total population size at time t is $n(t) = n_1(t) + \dots + n_k(t)$. The population structure at time t is defined as the column vector of proportions of individuals in the stages:

$$\mathbf{w}(t) = \left(\frac{n_1(t)}{n(t)}, \dots, \frac{n_k(t)}{n(t)} \right). \quad (8.8)$$

In fact, the dynamical properties of the discrete time system (Eq. 8.4) depend entirely on algebraic properties of the matrix. The main result is that the population grows (or decreases) at an *exponential rate*. More precisely, the population first goes through a transient regime of damped oscillations, followed by an asymptotic regime of exponential growth where

$$n(t+1) \approx \lambda n(t) \text{ for large } t. \quad (8.9)$$

Hence, the expected behavior of the structured model (Eq. 8.4) is close to that of the unstructured model (Eq. 8.1). The growth rate λ is the dominant eigenvalue of the matrix (Boxes 8.1 and 8.4). The asymptotic regime is reached concomitantly with the stabilization of the population structure:

$$\mathbf{w}(t) \rightarrow \mathbf{w}.$$

Box 8.1 The Life Cycle Graph and Dynamical Behavior

The existence of the dominant eigenvalue $\lambda > 0$ (a unique real eigenvalue of largest modulus), and the associated left and right positive eigenvectors \mathbf{v} and \mathbf{w} , is guaranteed under conditions pertaining to the structure of the life cycle graph, its stages and arcs, and not to the values associated with the arcs (the demographic parameters). The discrete dynamical system described by Eq. (8.4) is equivalent to performing paths of length t in the life cycle graph, traversing cycles from newborn stages via survival arcs and back to newborn stages via reproductive arcs. The condition of existence of the dominant eigenvalue λ is that the life cycle graph should be *irreducible* and *aperiodic*:

A) Irreducibility means the existence of an oriented path from any stage to any other. Reducibility occurs, for example, when postreproductive stages are included (Figure 8.1g; see also the case of source-sink metapopulations, Section 8.7). Such stages do not belong to reproductive cycles since newborn stages cannot be reached from them. They do not contribute to growth and can be omitted. In case of reducibility, there may nevertheless exist a dominant eigenvalue, in which case the main results still hold, but this is not

guaranteed, and the vectors \mathbf{v} and \mathbf{w} usually have some zero entries.

B) Aperiodicity means that the lengths of cycles in the life cycle graph have no common divisor > 1 . Periodicity occurs, for example, with the life cycle of Figure 8.1h, which produces survival-reproduction cycles of length 2, 4, 6, ..., when the life cycle is traversed 1, 2, 3... times: the common divisor is 2. The Leslie matrix is aperiodic (Figure 8.1d, assuming $m_i > 0$, but see also Figure 8.1i) because the cycle lengths have 1 as common divisor, hence are relatively prime. In case of periodicity, the population trajectories present periodic oscillations that are not damped, though the growth is still exponential on average. Aperiodicity is guaranteed when there is a self-loop (a cycle of length 1) in the life cycle graph, i.e. a nonzero entry on the diagonal of the matrix, a condition that is often met (e.g. Figure 8.1e, f).

Conditions (A) and (B) are equivalent to the matrix \mathbf{A} being primitive: there exists a positive integer q such that \mathbf{A}^q has all entries positive. To summarize, the generic behavior (primitive matrix) is the rule, with exceptions to be aware of: reducibility and periodicity, the latter being rare.

Here, the *stable stage distribution* $\mathbf{w} = (w_i)$, normalized $\sum w_i = 1$, is the right eigenvector associated with the eigenvalue λ . The proportion of individuals in stage i tends to w_i geometrically fast. The transient fluctuations depend on the initial population structure $\mathbf{w}(0)$. In fact, if $\mathbf{w}(0)$ equals \mathbf{w} , the asymptotic regime is attained instantly. The transient behavior is easily understood for an age-classified model. For example, if the initial condition is 100 individuals in the first (newborn) stage, and 0 individuals in the other stages, these 100 individuals traverse the pre-reproductive stages step by step (population size decreases); the surviving ones then reach the reproductive stages, from which the newborn stage is alimented again (population size bursts). We thus have oscillatory behavior until the number of individuals homogenize across stages to eventually meet the stable stage distribution.

Equation (8.2) generalizes into

$$\mathbf{n}(t) \approx C \lambda^t \mathbf{n}(0) \text{ for large } t. \quad (8.10)$$

Here, the constant term $C = \mathbf{v}\mathbf{w}(0)$ is the dot product of the reproductive value, the left eigenvector associated with the eigenvalue λ , a row vector $\mathbf{v} = (v_i)$, normalized $\sum v_i = 1$, and the initial population structure $\mathbf{w}(0)$.

The interpretation of the *reproductive value* can be understood from Eq. (8.10). The population grows exponentially at rate λ by Eq. (8.9), independently of the initial condition $\mathbf{n}(0)$. However, according to Eq. (8.10), population size depends on the initial structure $\mathbf{w}(0)$ and on the reproductive value \mathbf{v} : the stages i with large reproductive values v_i contribute most to population size (but not to the growth rate), weighted by the initial structure, as expressed by the dot product. For the Leslie matrix (Figure 8.1d), the typical pattern is that v_i increases up to age at first reproduction, because individuals have an increasing potential to contribute to future population size, and decreases thereafter.

The *transient oscillatory behavior* of the model should not be overlooked (Koons et al. 2007; Gamelon et al. 2014). Indeed, even if the population is at the demographic equilibrium, where the population structure is stationary, perturbations from the environment may alter the structure and drive the population into transient fluctuations.

Taking logs on each side of Eq. (8.10) provides an estimate of the growth rate:

$$\lambda \approx \exp\left(\frac{\ln(n(t)) - \ln(n(0))}{t}\right). \quad (8.11)$$

According to Eq. (8.11), if you observe a population at date t_0 and later on at date t_1 and measure population sizes $n_{obs}(t_0)$ and $n_{obs}(t_1)$, then the growth can be estimated by

$$\hat{\lambda} = \exp\left(\frac{\ln(n_{obs}(t_1)) - \ln(n_{obs}(t_0))}{t_1 - t_0}\right). \quad (8.12)$$

8.3.2 Demographic Descriptors

We have already encountered the growth rate λ which tells us if the demographic parameters of the population lead to increase ($\lambda > 1$) or decrease ($\lambda < 1$). The stable stage distribution \mathbf{w} and the reproductive value \mathbf{v} describe stage-specific contributions to the dynamics. For example, the population structure of introduced individuals should be chosen close to the stable stage distribution to avoid initial population fluctuations which could put the program at risk. If individuals in a single stage are introduced, those with the largest reproductive value should be preferred, since they contribute more to future population size.

In the age-classified model, let us consider an individual that survives up to age i and produces f_i offspring. The traversal of a survival-reproduction cycle in the life cycle graph can be associated with the cumulated rate

$$\phi_i = s_0 s_1 \cdots s_{i-1} f_i. \quad (8.13)$$

The *net reproductive rate*

$$R_0 = \sum_i \phi_i \quad (8.14)$$

represents the per individual contribution to the renewal of the population. The conditions $R_0 > 1$ and $\lambda > 1$ are equivalent.

The dominant eigenvalue λ is the largest root of the *characteristic equation* $\sum_i \phi_i X^{-i} = 1$, so that the terms

$$p_i = \phi_i \lambda^{-i} \quad (8.15)$$

satisfy $\sum p_i = 1$, hence constitute a probability distribution. A measure of the generation time is then defined as the mean of the distribution:

$$T = \sum_i i p_i. \quad (8.16)$$

By construction, T is the *mean age of the mothers*, assuming the population at the stable age distribution. *Entropy*, the Shannon diversity index of the p_i s,

$$S = - \sum_i p_i \ln(p_i), \quad (8.17)$$

is a measure of the complexity of the life cycle: it is linearly related to the logarithm of body size, metabolic rate, and

maximal life span (Demetrius et al. 2009). A semelparous life cycle has an entropy of zero (Figure 8.1h).

For the passerine model (Figure 8.1b, model file `pass_0.ulm`), the demographic parameter values are $s_0 = 0.2$, $s_1 = 0.35$, $s_2 = 0.5$ for survival, and $f_1 = f_2 = 7$ for fecundity, with primary sex ratio $\sigma = 0.5$. We obtain the growth rate $\lambda = 1.1050$ and generation time $T = 1.67$. For the wolf, survival rates are not known precisely in this population: various scenarios can be considered, from pessimistic to optimistic, leading to growth rates ranging from $\lambda = 0.93$ to $\lambda = 1.16$ (Figure 8.1c2, model file `wolf_0.ulm`).

Demographic descriptors can also be computed for models that are not age-classified. The analysis of the cycles subtending the life cycle graph allows us to compute the characteristic equation (of which λ is the largest root), and expressions for the eigenvectors \mathbf{w} and \mathbf{v} , and the net reproductive rate R_0 in terms of the demographic parameters (Caswell 2001). For size-classified models (Figure 8.1f), it can be convenient to translate the size currency into the more intuitive time currency. Simple formulas exist in this case, allowing, for example, to compute the *average residence time* in a stage (Barot et al. 2002). The general case for any nonnegative matrix that has relevant biological meaning is more complicated (Cochran and Ellner 1992). However, generation time has a simple expression (Bienvenu and Legendre 2015).

8.3.3 Sensitivities

When a parameter of the life cycle varies due to some condition, will the population still grow, or will it decrease? What change in a parameter will ensure the restoration of a declining population? These questions can be addressed using sensitivity analysis. The impact of small changes in the parameter x on the growth rate is measured by the *sensitivity* of λ to changes in x :

$$s_\lambda(x) = \frac{\partial \lambda}{\partial x}. \quad (8.18)$$

The meaning of the partial derivative is that if x changes by an amount Δx , then λ changes by an amount $\Delta \lambda = s_\lambda(x) \Delta x$. The sensitivity s_{ij} of λ to changes in the matrix entry a_{ij} is computed from the left and right eigenvectors by the formula

$$s_{ij} = \frac{v_i w_j}{\mathbf{v} \mathbf{w}} \quad (8.19)$$

where the denominator is a dot product. From the s_{ij} values, the sensitivity to changes in a lower level parameter x is obtained using the chain rule:

$$s_\lambda(x) = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x} = \sum_{i,j} s_{ij} \frac{\partial a_{ij}}{\partial x}. \quad (8.20)$$

Sensitivities of other demographic descriptors (e.g. T) or of the population vector entries can also be computed.

A related quantity is the *elasticity*, which measures proportional changes in a lower-level parameter (x):

$$e_\lambda(x) = \frac{x \partial \lambda}{\lambda \partial x}. \quad (8.21)$$

elasticities reflect (nonlinearly) the effects of proportional perturbations.

Sensitivities or elasticities allow us to determine the relative contribution of the demographic parameters to population growth (Box 8.2). In consequence, the most sensitive parameters should be determined with the greatest accuracy. Such parameters should be targeted

Box 8.2 Short-lived Versus Long-lived Species

The elasticity of λ to changes in a parameter c multiplying all reproductive transitions of the life cycle – the entries involving fecundities – is given by the inverse of the generation time (Houllier and Lebreton 1986; Bienvenu and Legendre 2015):

$$e_\lambda(c) = \frac{1}{T}. \quad (8.22)$$

This is the case of the primary sex ratio σ , or the juvenile survival s_0 in the age-classified model with prebreeding census (e.g. Figure 8.1b). As the elasticities sum to 1, the elasticity of λ to changes in a parameter d multiplying all nonreproductive transitions is given by

$$e_\lambda(d) = 1 - \frac{1}{T}. \quad (8.23)$$

The formula provides a rationale for the classification of species along the so-called fast-slow continuum. It leads to a useful dichotomy between short-lived and long-lived species. Typically, short-lived species (small T) with a fast life history (short life spans, large progeny sets, low adult survival) invest in reproduction, whereas long-lived species (large T) with a slow life history (long life spans, small progeny sets, high adult survival) invest in survival. In general, the most sensitive parameters of short-lived species

are the fecundities and the juvenile survival rate. The most sensitive parameters of long-lived species are the adult survival rates.

The generation time also reflects the tempo of biochemical reactions within the organism, measured by the metabolic rate P , and related to body mass W by the Kleiber allometric relation (Brown et al. 2004):

$$P \propto W^{3/4}. \quad (8.24)$$

Hence, the metabolic rate per unit mass,

$$\frac{P}{W} \propto W^{-1/4}, \quad (8.25)$$

decreases with increasing body mass. This is consistent with short-lived species having small body size and long-lived species, large body size. In a related way, it is observed that the rate of increase $r = \ln(\lambda)$ of natural populations verifies

$$r \approx \frac{\ln(R_0)}{T} \quad (8.26)$$

where R_0 is the net-reproductive rate, leading to the allometric relation:

$$r \propto T^{-1}. \quad (8.27)$$

If x changes by $\alpha\%$ then λ changes by $\beta\%$ with $\beta = \alpha e_\lambda(x)$. The elasticities e_{ij} of λ to changes in the matrix entries sum to 1. Zero entries in the population matrix usually have nonzero sensitivities, reflecting the impact a small change in these entries would have on λ , even if it is not biologically meaningful, but their elasticities are zero, as seen from the definition. Sensitivities and elasticities are generally positive, but may be negative. Indeed, as the growth rate obviously increases with an increase in survival or fecundity, these parameters have positive sensitivity. But if survival is written $s = 1 - m$, where m is mortality (Chapter 6), the parameter m has negative sensitivity. Sensitivities and elasticities provide similar information, that of a perturbation analysis: sensitivities reflect (linearly) the effects of additive perturbations;

to restore the growth of a population. Moreover, sensitivities quantify the change in specific parameters to reach a desired goal. Conversely, parameters with low sensitivities require less accuracy, as they contribute little to population dynamics.

Changes in matrix entries can be described by random variables A_{ij} with expectations given by the constant reference matrix \mathbf{A} , $E(A_{ij}) = a_{ij}$. The dominant eigenvalue of the corresponding random matrix is a random variable Λ such that $E(\Lambda) = \lambda$ (capital letters are used for random variables). Using the methods of Box 8.3, its variance is approximated using the sensitivities of \mathbf{A} :

$$\text{Var}(\Lambda) \approx \sum_{i,j,k,l} s_{ij} s_{kl} \text{Cov}(A_{ij}, A_{kl}). \quad (8.28)$$

Box 8.3 Environmental Stochasticity

Denoting $\lambda(\mathbf{M})$ the function associating to a matrix \mathbf{M} its dominant eigenvalue, a Taylor expansion to the first order gives

$$\lambda(\mathbf{M} + \Delta\mathbf{M}) \approx \lambda(\mathbf{M}) + \sum_{i,j} \frac{\partial \lambda(\mathbf{M})}{\partial m_{ij}} (\Delta\mathbf{M})_{ij} \quad (8.29)$$

where we recognize the sensitivities $s_{ij} = \frac{\partial \lambda}{\partial m_{ij}}$ under the sum. To account for environmental noise, we write

$$\mathbf{A} = \mathbf{A} + \mathbf{E} \text{ with } E(\mathbf{A}) = \mathbf{A} \text{ and } E(\mathbf{E}) = 0 \quad (8.30)$$

where the matrix $\mathbf{E} = (E_{ij})$ represents a small deviation $\Delta\mathbf{A}$ from matrix \mathbf{A} . Using the Taylor expansion above, the growth rate $\Lambda = \lambda(\mathbf{A}) = \lambda(\mathbf{A} + \mathbf{E})$ is a random variable such that

$$\Lambda \approx \lambda + \sum_{i,j} s_{ij} E_{ij}. \quad (8.31)$$

We have $E(\Lambda) = \lambda$ and

$$\text{Var}(\Lambda) \approx \sum_{i,j,k,l} s_{ij} s_{kl} \text{Cov}(E_{ij}, E_{kl}) = \sum_{i,j,k,l} s_{ij} s_{kl} \text{Cov}(A_{ij}, A_{kl}). \quad (8.32)$$

Tuljapurkar's formula (Tuljapurkar 1990) quantifies the impact of environmental noise on population growth depending on characteristics of the environmental process:

$$r_e \approx r - \frac{\sigma_e^2}{2\lambda^2} + \frac{\theta}{\lambda^2}. \quad (8.33)$$

Here, $r = \ln(\lambda)$ is the rate of increase in absence of stochasticity. The stochastic rate of increase r_e decreases linearly with the environmental variance σ_e^2 . The environmental variance is identified with the variance of Λ from variations in the matrix, as given by Eq. (8.32). It depends on changes in the entries of the mean matrix, quantified by the sensitivities, and on the covariance across matrix entries. Positive covariance is more detrimental than no covariance, whereas negative covariance is less. The alteration is (quadratically) less important with increasing λ . The term θ quantifies the contribution of temporal autocorrelation to stochastic growth. When there is no autocorrelation (iid environment), $\theta = 0$, and

$$r_e \approx r - \frac{\sigma_e^2}{2\lambda^2}. \quad (8.34)$$

When environmental variance is defined on the logarithmic scale as $\omega_e^2 = \text{Var}(\ln(\Lambda))$, we can write Eq. (8.32) with logarithms and use $\frac{\partial r}{\partial a_{ij}} = \frac{1}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$. Then Eq. (8.34) becomes.

$$r_e \approx r - \frac{1}{2} \omega_e^2, \text{ with } \omega_e^2 = \frac{\sigma_e^2}{\lambda^2}. \quad (8.35)$$

If the matrix entries vary independently:

$$\text{Var}(\Lambda) \approx \sum_{i,j} s_{ij}^2 \text{Var}(A_{ij}). \quad (8.36)$$

Similarly, if some lower level parameters x_i vary independently, the variance in growth rate is

$$\sigma_\lambda^2 \approx \sum_i \left(\frac{\partial \lambda}{\partial x_i} \right)^2 \sigma_{x_i}^2. \quad (8.37)$$

The formula allows us to compute confidence intervals on λ , given confidence intervals on measured parameter values. The distribution of Λ , which can be estimated using resampling methods (bootstrap; Caswell 2001), is generally skewed, but can often be approximated by a normal distribution. Under this assumption, the growth rate belongs to the interval

$$\lambda \pm 1.96\sigma_\lambda \text{ with a probability of 95\%,}$$

and more generally,

$$\lambda \pm z_\alpha \sigma_\lambda \text{ with a probability of } \alpha\%,$$

where z_α is the upper $\alpha/2$ percentage point of the standard normal distribution.

For the passerine model (file `pass_0.ulm`), the sensitivities of the growth rate to changes in the demographic parameters are $s_\lambda(s_0) = 3.309$, $s_\lambda(s_1) = 0.693$, $s_\lambda(s_2) = 0.401$ for survival, $s_\lambda(f_1) = 0.060$, $s_\lambda(f_2) = 0.035$ for fecundity. Juvenile survival s_0 is the most sensitive parameter in this short-lived species. It is checked for the elasticities, $e_\lambda(s_0) = e_\lambda(\sigma) = 1/T = 0.599$ (Box 8.2). We can also infer that if s_0 is known within $\sigma_{s_0} = 0.05$ then $0.78 \leq \lambda \leq 1.43$ with 95% confidence.

For the long-lived wolf (model file `wolf_0.ulm`), under the intermediate scenario ($\lambda = 1.085$), the parameter with the largest elasticity is the survival rate of the pack leaders, $e_\lambda(s_5) = 0.46$. The elasticity of fecundity is lower: $e_\lambda(f) = 0.14$.

8.4 Accounting for the Environment

The constant matrix model allows us to project the population if the conditions under which the demographic parameters have been measured were to be maintained.

The life cycle graph represents the genotype and part of the phenotype of an average individual. The part of the phenotype that is not accounted for in the constant matrix model depends on the influence of the biotic and abiotic environment on the life cycle. Three main phenomena are involved: (i) *density dependence* coming from the regulation of the demographic parameters by the limitation of resources; (ii) *environmental stochasticity* as the impact of variation in the environment on the demographic parameters, considered as random processes; and (iii) *spatial structure*, where subpopulations are connected by dispersal.

8.5 Density Dependence

All populations have the potential to grow exponentially, which is what the constant matrix model shows (Section 8.3.1). However, exponential growth cannot be sustained forever because living organisms depend on finite resources. Density dependence – the fact that population growth has to decrease with increasing population density – comes from *intra-specific competition* for resources (nutriment, space, mate), but may also come from *inter-specific competition* for shared resources, or even from predation (more prey sustain more predators, in turn decreasing the growth of the prey). Here, we restrict ourselves to the point of view of the population, and density dependence is basically described by a unique parameter, the carrying capacity K .

8.5.1 Density-dependent Scalar Models

A continuous time formulation of the unstructured model (8.1) is

$$\frac{1}{n} \frac{dn}{dt} = r. \quad (8.38)$$

The increase of the population is $\frac{dn}{dt}$, and the per individual rate of increase, $\frac{1}{n} \frac{dn}{dt}$, is the constant r . The differential equation is integrated as

$$n(t) = e^{rt} n(0). \quad (8.39)$$

By identification with Eq. (8.2), we obtain a relation between the rate of increase r and the growth rate:

$$\lambda = \exp(r). \quad (8.40)$$

The increase versus decrease criterion, $\lambda > 1$ versus $\lambda < 1$, translates into $r > 0$ versus $r < 0$.

To account for density dependence, one assumes that the rate of increase is maximal, equal to r , when

population size is 0, decreases linearly with increasing population size, and is < 0 when population size is above the carrying capacity K , the largest number of individuals that the environment can accommodate. Hence,

$$\frac{1}{n} \frac{dn}{dt} = r \left(1 - \frac{n}{K} \right). \quad (8.41)$$

The integration of the differential equation leads to the so-called logistic equation. Here, in our discrete time context, using Eq. (8.40), we may write the density-dependent growth rate as

$$\lambda_K(n) = \exp \left(r \left(1 - \frac{n}{K} \right) \right), \quad (8.42)$$

which leads to the Ricker equation:

$$n(t+1) = \lambda \exp \left(-\frac{r}{K} n(t) \right) n(t). \quad (8.43)$$

(I do not claim that this equation is equivalent to the logistic equation.)

More generally, to account for density dependence, we make the growth rate decrease with increasing population size via some function f :

$$n(t+1) = \lambda f(n(t)) n(t). \quad (8.44)$$

8.5.2 Density-dependent Matrix Models

In a density-dependent matrix model, some of the matrix entries are regulated by population sizes in the stages. The projection equation is

$$\mathbf{n}(t+1) = \mathbf{A}(\mathbf{n}(t)) \mathbf{n}(t). \quad (8.45)$$

For example, the demographic parameter x regulated by the Ricker function is

$$x_{reg} = \exp(-(\alpha_1 n_1 + \dots + \alpha_k n_k)) x \quad (8.46)$$

where the coefficients $\alpha_1, \dots, \alpha_k$, some of which may be 0, express the relative contribution of the stages to resource consumption. Contrarily to the unstructured model, the carrying capacity K is not apparent in this formulation. The coefficients α_i must be adjusted in order to match a pre-defined carrying capacity.

The Ricker function $f(n) = \exp(-\alpha n)$ is overcompensatory in the sense that a population overshooting the carrying capacity will be penalized by a large decrease. Other regulation function can be used, for example, the compensatory function $f(n) = \frac{1}{1 + \beta n}$, for which decrease will compensate the increase.

Under density dependence, the long-term growth rate of the regulated population is 1 on average. The expected dynamical behavior is that the population increases up

to the carrying capacity and then stabilizes (single point equilibrium). The trajectory then presents an S-shaped (sigmoid) pattern. However, complex dynamics can occur, and more easily when the growth rate λ (in absence of regulation) is large. Indeed, when λ is large, the population will overshoot the carrying capacity more importantly, creating a stronger feedback regulation. For not-too-large λ , damped oscillations result, and population size equilibrates back to the carrying capacity. For large λ , oscillations may not damp because of strong growth as soon as density-dependent regulation is relaxed. This can produce periodic, quasi-periodic, or chaotic dynamics.

Density dependence can also be incorporated without altering the matrix, but considering the carrying capacity K as a ceiling. If the model predicts $n(t+1) > K$, then we set $n(t+1) = K$: the population sizes in the stages are reduced in some proportion (for example, proportionately to the stable stage distribution) so that they sum up to K .

It is often assumed that small populations are far from the carrying capacity, so that density dependence need not be modeled. This is, however, not always the case (Mugabo et al. 2013). For example, observed probabilities of extinction in small populations of spiders could not be recovered without incorporating density dependence (Schoener et al. 2003). It was also shown in this study that population structure cannot be disregarded at small population sizes.

8.5.3 Parameterizing Density Dependence

Using the observed population sizes $n(t)$ along time, the model of population regulation can be fit to the data using linear or nonlinear regression of the growth rate at time t : $\lambda_t = n(t+1)/n(t)$ against $n(t)$. The procedure gives the best function f such that $\lambda_t = \lambda f(n(t))$ (Morris and Doak 2002). For the Ricker model, $f(n) = \exp(-an)$.

8.5.4 Density-dependent Sensitivities

It is possible to compute the sensitivity or elasticity of the equilibrium population size n_{eq} , or of an average of population size over some time period in case of complex dynamics, to changes in a parameter x (Grant and Benton 2000, 2003; Caswell et al. 2004).

8.6 Environmental Stochasticity

Environmental stochasticity refers to the impact of the environment on the population due to biotic interactions (e.g. competing species, predators) or abiotic factors (e.g. temperature), considered as a random

process. Models for the environment range from *environmental noise*, repeatedly deviating the vital rates from their average values, to rare *catastrophic events* significantly altering these values. The demographic parameters affected by the environment are now considered as random variables, defined according to the model chosen for the environment. Population size is a random variable, N , and the population matrix a random matrix \mathbf{A} . Under generic conditions of *ergodicity*, which essentially means that past events are progressively forgotten by the process so that initial conditions are not determinant for the long-term dynamics, population size N admits an asymptotic distribution whose mean and variance bring information on the influence of the environment on the dynamics.

8.6.1 Models of the Environment

- I) In the simplest form of a stochastic environment, the values along time of a parameter impacted by the environment are drawn from a fixed probability distribution, with mean the reference value of the parameter. Each value is drawn independently of the previous values with no temporal autocorrelation. Hence, the random variables X_t describing the variations of the parameter x over time t are *independent and identically distributed* (iid). For example, the impact of the environment on fecundity f is modeled by drawing the stochastic fecundities along time according to the normal distribution:

$$f_e \equiv N^+(f, \sigma_f). \quad (8.47)$$

Here, the $+$ sign indicates that only nonnegative values are kept (as fecundity cannot be negative), and σ_f is the standard deviation, measuring the impact of environmental stochasticity on f . A similar approach is taken for survival rates, where the random values are constrained in the interval $[0,1]$. A beta distribution can be used in this case.

- II) A *Markovian environment* accounts for *temporal autocorrelation* where the outcome of an event at a given date depends on previous outcomes. In the iid environment, no memory is kept of previous outcomes of the random parameters, as when casting a die. However, environmental variables often exhibit positive autocorrelation. For example, temperatures in May in one year tend to follow temperatures in May the previous year. To give an example of the Markovian environment, assume that there are good years (G) and bad years (B), and that the parameter X has value x_G in G-years and value x_B in B-years (with $x_G > x_B$). Assume that G-years and B-years are equiprobable. We parameterize positive autocorrelation

in the environment (i.e. G-years are more likely to be followed by G-years) by α , $0 \leq \alpha \leq 0.5$, and use a two-states Markov chain. The states occur with the same frequency, 0.5. Switching states occurs with probability α , and remaining in the same state occurs with probability $1 - \alpha$, as described by the Markov matrix:

$$\begin{bmatrix} 1-\alpha & \alpha \\ \alpha & 1-\alpha \end{bmatrix}. \quad (8.48)$$

Hence, a low value of α means a strong autocorrelation. As α increases, the strength of autocorrelation decreases, and $\alpha = 0.5$ corresponds to no autocorrelation. For $\alpha > 0.5$, we have negative autocorrelation (switching states is more likely). More generally an autocorrelated environment can be modeled by a finite state Markov chain and a population matrix associated with each state (Cohen 1977; Caswell and Kaye 2001; Tuljapurkar and Haridas 2006). At each time step, an environmental state is drawn using the Markov chain, and the corresponding matrix is used in the projection equation.

A simple way to implement temporal autocorrelation is to use an autoregressive process of order 1 to update a parameter X with mean μ and variance σ^2 :

$$X(t+1) = \alpha(X(t) - \mu) + B(t), \quad (8.49)$$

where $B(t)$ is iid with mean μ and variance $\sigma^2(1 - \alpha^2)$. Autocorrelation is parameterized by α , $-1 \leq \alpha \leq 1$, with positive autocorrelation for $\alpha > 0$ (see model file `pass_ea.ulm`).

- III) *Catastrophic events* can be modeled by an occurrence frequency and a given impact. For example, when a catastrophe occurs, some parameters are reduced to 50% of their reference value, or total population size is reduced to a given proportion. Catastrophes may also present temporal autocorrelation. Population dynamics under catastrophic regimes (large deviations) are less known theoretically, but can be easily simulated (Lande 1993).

At a given time step, different demographic parameters affected by the environment may covary due to joint effects of environmental conditions, or to life-history tradeoffs. For example, a random reduction in survival is associated with a reduction in fecundity (positive covariance), or, less likely, with an increase in fecundity (negative covariance).

8.6.2 Stochastic Dynamics

Under environmental stochasticity, the population matrix is stochastic, depending on t , so that the

deterministic model for constant conditions (Eq. 8.4) is now written with a stochastic population vector as:

$$\mathbf{N}(t+1) = \mathbf{A}_t \mathbf{N}(t). \quad (8.50)$$

A *population trajectory* is a realization of this random process. Underlying the process is the constant matrix \mathbf{A} , with $E(\mathbf{A}_t) = \mathbf{A}$ in case of environmental noise (environments I and II above).

Population growth is a multiplicative process, here affected at each time step by random events. It can be shown by the multiplicative version of the central limit theorem that the distribution of total population size, $N(t)$, is lognormal meaning that $\ln(N(t))$ is normally distributed. Hence, it is convenient to use the logarithmic scale. Eq. (8.11) shows that, for a constant matrix \mathbf{A} :

$$\lambda = \lim_{t \rightarrow \infty} n(t)^{\frac{1}{t}}, \text{ giving } r = \ln(\lambda) = \lim_{t \rightarrow \infty} \frac{1}{t} \ln(n(t)). \quad (8.51)$$

The formula indicates that the *stochastic rate of increase* can be defined as

$$r_e = \lim_{t \rightarrow \infty} \frac{1}{t} E[\ln(N(t))], \quad (8.52)$$

and the *environmental variance* can be calculated as $\omega_e^2 = \lim_{t \rightarrow \infty} \frac{1}{t} \text{Var}[\ln(N(t))]$. It can be demonstrated that these are indeed the relevant descriptors (Caswell 2001). The rate r_e is in general less than the rate $r = \ln(\lambda)$ in absence of environmental stochasticity, the difference increasing with variance in the environment (Box 8.3). The logarithm of population size, $\ln(N(t))$, is normally distributed with mean $r_e t$ and variance $\omega_e^2 t$. Thus, the mean of $\ln(N)$ increases or decreases linearly with time, depending on $r_e > 0$ or $r_e < 0$, and the distribution of $\ln(N)$ spreads over time, with linearly increasing variance (Morris and Doak 2002). Consequently, the mean of population size $N(t)$ increases or decreases exponentially with time, and its variance increases exponentially.

To summarize, the stochastic matrix model keeps on average the exponential behavior of the underlying constant model, at rate $\lambda_e = \exp(r_e) < \lambda$, but random fluctuations create opportunity for extinction. Stochasticity may entail negative growth, hence certain extinction in the long run even when the underlying constant model has positive growth. In this latter case, the mean values of the demographic parameters entail positive growth, but fluctuations around these values may produce negative growth on average: the threshold depends on the intensity of the fluctuations, namely on the environmental variance (Box 8.3).

If the *probability of extinction* is plotted against time, the typical pattern is an S-shaped curve. The curve starts from 0 at $t = 0$, then increases to eventually plateau at the

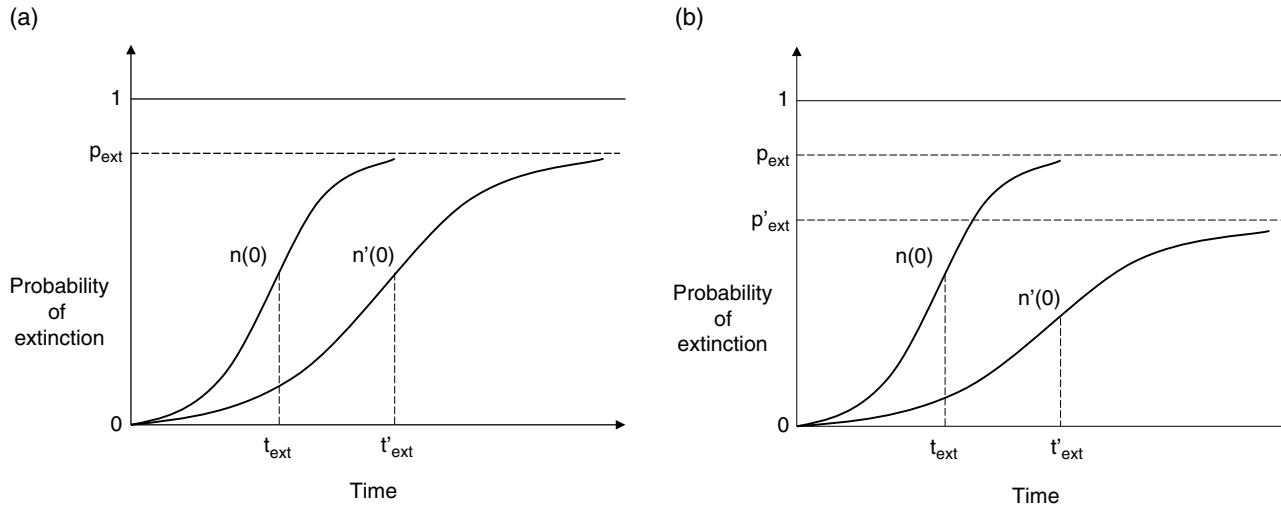


Figure 8.2 Schematic representation of the probability of extinction along time: p_{ext} is the ultimate probability of extinction, t_{ext} the mean time to extinction, and $n(0) < n'(0)$ is the initial population size. (a) Environmental stochasticity: the ultimate probability of extinction is independent of initial population size, the mean time to extinction increases with increasing initial population size. (b) Demographic stochasticity: the probability of extinction increases with decreasing population size, the mean time to extinction increases with increasing population size.

ultimate probability of extinction for large t . The portion of the curve where the probability of extinction increases sharply corresponds to the mean time to extinction. An important feature of environmental stochasticity is that the ultimate probability of extinction where the extinction curve plateaus does not depend on the initial population size $n(0)$. However, the mean time to extinction does, the extinction curve shifting to the left with decreasing $n(0)$ so that the ultimate probability of extinction is reached sooner (Figure 8.2a).

From a computational point of view, stochastic processes are best studied using Monte Carlo simulation (Box 8.6). A large number m of trajectories (e.g. $m = 1000$) are drawn up to some time horizon, and statistics are performed on the set of trajectories. The trajectories that go below a predefined threshold h at time τ (i.e. $n(\tau) < h$) are declared extinct, with associated extinction time τ . Usually the threshold $h = 1$ is used. Larger values of h (e.g. $h = 50$) define a *quasi-extinction threshold*. The probability of extinction at time t , $p_{ext}(t)$, is estimated as the proportion of the m trajectories going extinct at time $\tau \leq t$. The extinction time is estimated as the mean value of the extinction times of the extinct trajectories. Quasi-extinction thresholds and probabilities provide estimates of *minimum viable population sizes*, a mainstay of *Population Viability Analysis* (PVA, Boyce 1992). Denoting $n^{(i)}(t)$ the i -th trajectory of the Monte Carlo simulation, the expected population size along time, $E(N(t))$, is estimated by the average trajectory

$$\bar{n}(t) = \frac{1}{m} \sum_{i=1}^m n^{(i)}(t). \quad (8.53)$$

The mean population size over non-extinct trajectories, $E(N(t)|N(t) > h)$, can also be computed. The *stochastic rate of increase* is estimated using:

$$r_e = \frac{1}{m} \sum_{i=1}^m \frac{\ln(n^{(i)}(t)) - \ln(n(0))}{t}. \quad (8.54)$$

Underlying this computation is the meaning of ergodicity: the long-term time average of a quantity over a single trajectory can be estimated using the short-term average over a large number of trajectories.

For the passerine model, let us consider that juvenile survival s_0 is subjected to random fluctuations under an iid model of the environment. We use a beta distribution, here parameterized according to mean and standard deviation: $s_{0e} \equiv \text{Beta}(s_0, \sigma_{s_0})$, with the reference value $s_0 = 0.2$ and $\sigma_{s_0} = 0.15$. Monte Carlo simulation up to time 50 is run over 10,000 trajectories with 20 individuals as initial population size, 10 subadults and 10 adults, close to the stable age distribution. At time 50, the stochastic growth rate is $\lambda_e = 1.008$, the probability of extinction (threshold $h = 1$) is $p_{ext}(50) = 0.25$, the mean time to extinction is $t_{ext}(50) = 7$ years, the mean time to extinction over non-extinct trajectories is $t_{ext}^*(50) = 28$ years. We observe that small fluctuations in the most sensitive parameter s_0 reduce the growth rate by 10% (from $\lambda = 1.1050$ to $\lambda_e = 1.008$) and produce a large probability of extinction with important disparity across trajectories. The probability of quasi-extinction with threshold $h = 10$ at time 50 is $q_{ext}(50) = 0.73$ (model file `pass_e.ulm`).

Box 8.4 Computing the Growth Rate

The algorithm uses the fact that $\frac{n(t+1)}{n(t)} \rightarrow \lambda$ is geometrically fast when iterating Eq. (8.4) (power method). In the following, \mathbf{w}, \mathbf{w}' are vectors for the population structure, \mathbf{v}, \mathbf{v}' are vectors for the reproductive value, and \mathbf{A} is the $k \times k$ projection matrix, assumed primitive (Box 8.1). The norm of a vector \mathbf{u} is defined as $|\mathbf{u}| = \sum_i u_i$. The algorithm stops when successive values of λ are within $\varepsilon = 10^{-9}$ (or when t is above some time horizon $t_{\max} = 10\,000$, in which case it fails).

$\mathbf{w} \leftarrow [1/k, \dots, 1/k]$ initial value of population structure

$\mathbf{v} \leftarrow [1/k, \dots, 1/k]$ initial value of reproductive value

$\lambda \leftarrow 1$

$t \leftarrow 0$

repeat

$t \leftarrow t + 1$ increment time

$\mathbf{w}' \leftarrow \mathbf{A}\mathbf{w}$ update population structure

$norm \leftarrow |\mathbf{w}'|$ compute norm

$\mathbf{w} \leftarrow \mathbf{w}'/norm$ rescale population structure

$\lambda_1 \leftarrow \lambda$ memorize previous value of λ

$\lambda \leftarrow norm$ update λ

$\mathbf{v}' \leftarrow \mathbf{v}\mathbf{A}$ update reproductive value

$norm \leftarrow |\mathbf{v}'|$ compute norm

$\mathbf{v} \leftarrow \mathbf{v}'/norm$ rescale reproductive value

until $|\lambda - \lambda_1| < \varepsilon$ or $t > t_{\max}$.

At the end of the algorithm, λ contains the dominant eigenvalue, \mathbf{w} the stable population structure, and \mathbf{v} the reproductive value.

Box 8.5 Environmental Variance and Demographic Variance

Engen et al. (1998) apply the law of total variance to the stochastic contribution W of a female individual to population size at the next time step, given the environment Z :

$$\text{Var}(W) = \text{E}(\text{Var}(W|Z)) + \text{Var}(\text{E}(W|Z)). \quad (8.55)$$

This can be interpreted as

$$\text{Var}(W) = \sigma_d^2 + \sigma_e^2, \quad (8.56)$$

where demographic variance $\sigma_d^2 = \text{E}(\text{Var}(W|Z))$ is the mean through time of the variance of individual contributions to population size from a time step to the next, and environmental variance $\sigma_e^2 = \text{Var}(\text{E}(W|Z))$ is the variance through time of the mean individual contribution to population size from a time step to the next.

The stochastic population matrix can be decomposed $\mathbf{A} = \mathbf{E} + \mathbf{D}$ according to two sources of stochasticity, the environment represented by \mathbf{E} and demographic stochasticity represented by \mathbf{D} . It is assumed that there is no covariance between \mathbf{E} and \mathbf{D} , and that they have 0 expectation. The methods of Box 8.3 lead to (Engen et al. 2005):

$$\sigma_e^2 = \text{Var}(\mathbf{E}|N) \approx \sum_{i,j,k,l} s_{ij}s_{kl} \text{Cov}(E_{ij}, E_{kl}), \quad (8.57)$$

$$\sigma_d^2 = \text{Var}(\mathbf{D}|N) \approx \sum_{i,j,k,l} s_{ij}s_{kl} \text{Cov}(D_{ij}, D_{kl}). \quad (8.58)$$

The total variance in the stochastic growth rate Λ is then

$$\text{Var}(\Lambda|N) = \sigma_e^2 + \frac{\sigma_d^2}{N}. \quad (8.59)$$

The formula highlights the $1/N$ dependency of the variance in Λ with respect to demographic stochasticity. The corresponding variance in population size is

$$\text{Var}(N(t+1)|N(t)=N) = \sigma_e^2 N^2 + \sigma_d^2 N. \quad (8.60)$$

Hence, although environmental variance is usually smaller than demographic variance, the environmental term dominates for large populations. Demographic stochasticity can in fact be neglected when $N \gg \frac{\sigma_d^2}{\sigma_e^2}$ (Lande et al. 2003).

The stochastic rate of increase (environmental plus demographic stochasticity) can be written:

$$s(N) \approx r - \frac{\sigma_e^2}{2\lambda^2} - \frac{\sigma_d^2}{2\lambda^2 N}, \quad (8.61)$$

where the negative impact of the environment agrees with Eq. (8.34). The environmental and demographic variances can be estimated from individual data, provided that the dataset is large enough (Engen et al. 2005). The preceding results also hold when demographic stochasticity is replaced by demographic heterogeneity (Vindenes et al. 2008).

8.6.3 Parameterizing Environmental Stochasticity

The value of the variance σ_X^2 of a random parameter X can be estimated from the observed time series of the parameter, and put in relation with known environmental conditions on the site, such as a time series of temperatures. Environmental variance σ_e^2 can also be recovered from individual data using the methods of Engen et al. (2005) (Box 8.5).

More generally, environmental stochasticity can be introduced to test the robustness of the species and estimate its probability of extinction, without precise reference to the environment. The strength of environmental noise can be parameterized from low to high to produce various scenarios. A rule of thumb is that $\sigma_X \approx 0.3E(X)$ in natural populations (Mills et al. 1996).

8.7 Spatial Structure

Populations are in general not closed, but subject to immigration and emigration. A *metapopulation* is a set of populations of the same species living on separate sites connected by dispersal from one site to another (Morris and Doak 2002). In a metapopulation, a local population going extinct may start again through recolonization from neighboring sites, ensuring the persistence of the metapopulation (rescue effect). The metapopulation framework can, to a certain extent, be studied using matrix models. Demographic descriptors generalizing those of Section 8.5 can be computed for constant age-

classified multisite matrix models (Lebreton 1996). A simple example is given in Figure 8.1j, where an age-classified model is connected from a stage I representing the pool of immigrants, and to a stage E representing the pool of emigrants. To account for space, matrix population models can also be incorporated into *diffusion models*, for example, to study expanding waves of invading species (Neubert and Caswell 2000). They could also underlie the local rules of cellular automata.

We use the passerine model to show counterintuitive features of metapopulation demography (model file `pass_ab.ulm`). Figure 8.1k presents the life cycle graph of two passerine populations living on sites A and B, with juveniles dispersing from A to B at rate m_{AB} and from B to A at rate m_{BA} .

We first assume that the two populations have the same reference demographic parameters so that their growth rates are identical: $\lambda_A = \lambda_B = 1.1050$. With the dispersal rates $m_{AB} = 0.2$, $m_{BA} = 0.2$, the growth rate of the metapopulation is $\lambda = 1.0978$, slightly lower than in absence of dispersal. The A-entries and the B-entries of the metapopulation age structure and reproductive value vector are identical and positive. When the dispersal rates are $m_{AB} = 0.2$, $m_{BA} = 0$ (no dispersal from B to A, the matrix is reducible, see Box 8.1), the growth rate of the metapopulation is $\lambda = \lambda_A = 1.1050$. In this case, the A-entries of the metapopulation structure are 0 because the A-population is depopulated; the entries of the metapopulation reproductive value are all positive, those of the B-population being larger than those of the A-population.

Box 8.6 Monte Carlo Simulation

The Monte Carlo simulation casts m trajectories up to some time horizon t_{\max} . We compute the average population size $\bar{n}(t)$ along time, the stochastic rate of increase r_e , and the probability of quasi-extinction p_{ext} with threshold h at time t_{\max} .

In the following, \mathbf{n} is the population vector, $|\mathbf{n}| = \sum_i n_i$ is population size, \mathbf{A} is a trajectory-specific realization of the stochastic projection matrix \mathbf{A} , and $\bar{\mathbf{n}}$ is a vector of size at least t_{\max} for computing the average population size along time.

```
for  $t \leftarrow 1$  to  $t_{\max}$  do  $\bar{\mathbf{n}}[t] \leftarrow 0$  initialize average trajectory
 $\text{ext} \leftarrow 0$  initialize number of extinctions
 $r_e \leftarrow 0$  initialize stochastic rate of increase
for  $i \leftarrow 1$  to  $m$  do loop over trajectories
  SetSeed( $i$ ) set random generator seed to trajectory-specific value
   $\mathbf{n} \leftarrow \mathbf{n}_0$  initialize population vector
```

```
 $n_0 \leftarrow |\mathbf{n}|$  memorize initial population size
for  $t \leftarrow 1$  to  $t_{\max}$  do loop over time
   $\mathbf{n} \leftarrow \mathbf{A}\mathbf{n}$  update population vector
   $n \leftarrow |\mathbf{n}|$  compute population size
  if  $n < h$  then  $\text{ext} \leftarrow \text{ext} + 1$  quasi-extinction
endloop
 $r_e \leftarrow r_e + (\ln(n) - \ln(n_0))/t_{\max}$  update stochastic rate of increase
endloop
for  $t \leftarrow 1$  to  $t_{\max}$  do  $\bar{\mathbf{n}}[t] \leftarrow \bar{\mathbf{n}}[t]/m$  compute average trajectory
 $p_{\text{ext}} \leftarrow \text{ext}/m$  probability of extinction
 $r_e \leftarrow r_e/m$  stochastic rate of increase
```

Note that a trajectory declared quasi-extinct is nevertheless computed up to t_{\max} , hence contributes to the average trajectory $\bar{\mathbf{n}}$, and to the stochastic rate r_e .

We now assume that the B-population is decreasing, with reduced fecundities ($f_{B1} = 5$, $f_{B2} = 6$, leading to $\lambda_B = 0.9582$). When the dispersal rates are $m_{AB} = m_{BA} = 0.2$, the metapopulation growth rate is altered, $\lambda = 1.0651$, the A-entries of the metapopulation structure are larger than the B-entries, and a similar pattern holds for reproductive values. When the dispersal rates are $m_{AB} = 0.2$, $m_{BA} = 0$, we are in the case of a source-sink metapopulation. The metapopulation growth rate is further altered, $\lambda = 1.0539$, the A-entries of the metapopulation structure are larger than the B-entries, and the B-entries of the metapopulation reproductive value are 0 because the B-population does not contribute to growth. When the dispersal rates are $m_{AB} = 0$, $m_{BA} = 0.2$, juveniles disperse from the decreasing population to the increasing one. The metapopulation growth rate is $\lambda = \lambda_A = 1.1050$, the B-entries of the metapopulation structure are 0, and the A-entries of the metapopulation reproductive value are larger than the B-entries.

8.8 Demographic Stochasticity

Demographic stochasticity is the chance realization of the transitions in the life cycle graph by individuals. Demographic stochasticity is an intrinsic feature of the demographic process, independent of the environment. Moreover, it is unavoidable. As we shall see, the effects of demographic stochasticity are only sensible when population size is small, but the contribution to the extinction risk can be important for small populations.

8.8.1 Branching Processes

We still assume the individuals are identical, but account for heterogeneity in their fates; that is, different realizations of their vital rates. *Demographic heterogeneity*, where individuals are not assumed to be identical, accounts for different realizations of heterogeneous life cycles (Section 8.9).

In the life cycle graph, when n individuals survive from one stage to the next, say with rate s , some of them may either survive (with probability s) or die (with probability $1 - s$). The number n' of survivors is the sum of n draws of the Bernoulli (head and tail) distribution with parameter s , or equivalently, a single draw according to the binomial distribution:

$$n' \equiv \text{Binom}(n, s). \quad (8.62)$$

Every 0/1 transition (sex determination, dispersal status) can be treated in the same way. Similarly, when n individuals reproduce with fecundity rate f , the number n' of offspring is the sum of n draws of the Poisson distribution with parameter f , which we denote as

$$n' \equiv \text{Poisson}(n, f). \quad (8.63)$$

Integer distributions other than the Poisson distribution can be used for reproduction.

The above described randomization of the life cycle events amounts to constructing a branching process on the relations associated with the life cycle graph (Eq. 8.3). For the passerine model, the relations of the branching process built from the matrix relations are:

$$n_1(t+1) = \text{Binom}(\text{Poisson}(n_1(t), f_1) + \text{Poisson}(n_2(t), f_2), \sigma s_0), \quad (8.64)$$

$$n_2(t+1) = \text{Binom}(n_1(t), s_1) + \text{Binom}(n_2(t), s_2). \quad (8.65)$$

In the framework of demographic stochasticity, population sizes are integer numbers. The population is extinct as soon as its size is 0. Even when $\lambda > 1$, the probability of extinction is nonzero. Indeed, there is a nonzero probability that all individuals in a stage do not survive or do not reproduce. Such an event is rare when population size is large. Hence, demographic stochasticity mostly plays at small population sizes. This moreover suggests that at large population size, with or without demographic stochasticity, dynamical behaviors will be close. When incorporating demographic stochasticity, the average behavior of the random process is that of the constant underlying model, with exponential growth or decrease at rate λ and average population structure \mathbf{w} . The behavior differs for the probability of extinction. In the constant model, the probability of extinction is 1 when $\lambda < 1$, and 0 when $\lambda \geq 1$. Under demographic stochasticity, the probability of extinction is 1 when $\lambda \leq 1$, and has a definite nonzero value when $\lambda > 1$.

Denoting $q_i(t)$ the probability of extinction at time t when the initial population consists in a single individual in stage i , the probability of extinction at time t when the initial population consist in $n_i(0)$ individuals in stage i is

$$p(t) = q_i(t)^{n_i(0)}. \quad (8.66)$$

If $q_i(t) = 1$, certain extinction occurs. If $q_i(t) < 1$, the above relation shows that the extinction risk from demographic stochasticity decreases exponentially with increasing population size. The overall probability of extinction at time t is

$$p(t) = q_1(t)^{n_1(0)} \dots q_k(t)^{n_k(0)}, \quad (8.67)$$

depending on initial population size and structure. The ultimate probability of extinction is

$$p = \lim_{t \rightarrow \infty} p(t). \quad (8.68)$$

When $\lambda \leq 1$ in the underlying constant matrix model, we have certain extinction under demographic

stochasticity (in finite time for $\lambda < 1$, and in infinite expected time for $\lambda = 1$). The probability of extinction along time presents an S-shaped pattern, as for environmental stochasticity. However, under demographic stochasticity, for $\lambda > 1$ the curve plateaus at a value which depends on initial population size, whereas this is not the case for environmental stochasticity (Figure 8.2b).

8.8.2 Two-sex Models

When population size is small (say less than 50–100 individuals), each individual behavior matters, and demographic stochasticity can be an important factor of the extinction risk. Individual fitness may decrease at low population density due to the deterioration of social bonds or cooperative behavior, a phenomenon known as the *Allee effect* (Courchamp et al. 1999, 2008). An important driver of the Allee effect comes from the mating system which relies on behavior (sexual selection, Andersson 1994), but it is also sensitive to demographic stochasticity acting on the number of males and females (Bessa-Gomes et al. 2004).

Consider a population of males and females with monogamous pair formation and primary 1 : 1 sex ratio where the proportion of females at birth is 0.5. Computation shows that, because of demographic stochasticity alone, the probability of an individual being mated is 0.9 when there are 100 individuals, but drops to 0.75 when there are 10 individuals. The probability drops even further if females are choosy due to sexual selection, and to 0.55 when population size is 10 (Møller and Legendre 2001). For small populations with sexual reproduction, the male portion of the population cannot be ignored, even if the male and female life cycles are identical. The population is doomed to extinction when there are either no males or no females left, a situation which can occur because of demographic stochasticity. Hence, for small populations, two-sex models are recommended. For example, observed probabilities of extinction in the polygynous bighorn sheep *Ovis canadensis* could not be reconstructed using a model based on females only (Legendre 2004).

Two-sex models incorporate the life cycle of males, which may differ from the life cycle of females, notably in the case of sexual dimorphism. In the two-sex life cycle (Figure 8.11), the male and female parts are coupled by the pair formation process. The mating process is modeled using a function giving the number of matings at a given time. For example, the monogamous mating function

$$\mu(f, m) = \min(f, m) \quad (8.69)$$

counts the maximum number of monogamous pairs that can be formed given the number of reproductive males (m) and females (f). The polygynous mating function:

$$\mu(f, m) = \min(f, hm) \quad (8.70)$$

gives the number of matings when each male mates on average with h females, h being harem size. The *breeding sex ratio* is the proportion of reproductive females in the reproductive population at a given time:

$$\rho = \frac{f}{m+f}. \quad (8.71)$$

We have $\frac{\min(f, hm)}{f+m} = \min\left(\frac{f}{f+m}, \frac{hm}{f+m}\right) = \min(\rho, h(1-\rho))$, so that the optimal breeding sex ratio is obtained when $\rho = h(1-\rho)$, or

$$\rho_{opt} = \frac{h}{h+1}. \quad (8.72)$$

For monogamy, $\rho_{opt} = 0.5$, as expected. Care must be taken to appropriately design the mating function (Bessa-Gomes et al. 2010).

The mating function introduces a nonlinearity in the underlying constant model which becomes *frequency dependent*, depending on the relative proportions of each sex (Caswell and Weeks 1986). The generic behavior is nevertheless that of exponential growth after transient fluctuations. However, in the two-sex model, transient fluctuations come from both the convergence toward the stable stage distribution and toward the stable sex structure, where the breeding sex ratio becomes constant. The transient fluctuations in sex structure superimposed on those in stage structure suggest that the two-sex model under demographic stochasticity leads to a larger extinction risk than the corresponding female-based model (although fluctuations could cancel one another in some instances). This is indeed the case, and the effect is more pronounced for short-lived species (Legendre et al. 1999), in which parameters associated with reproductive transitions are more sensitive (Box 8.2). Moreover, the growth rate λ_μ of the two-sex model with mating function μ verifies $\lambda_\mu \leq \lambda$. The difference between the two-sex growth rate λ_μ and the female-based growth rate λ depends on how far the realized breeding sex ratio ρ is from the optimal one ρ_{opt} (Legendre 2004). A two-sex model for passerines with monogamous pair formation (Figure 8.11), and incorporating demographic stochasticity, is given in model file `pass_2d.ulm`.

8.9 Demographic Heterogeneity

Demographic heterogeneity accounts for the fact that individuals in a population are not identical. Individuals can differ genetically, by their ontogenic trajectories, and by the plastic adaptation of their phenotypes to heterogeneous environmental pressures, possibly involving

epigenetics. In addition, social status and behavior may vary over time. Figure 8.1m displays a simple example: newborn individuals j in stage 1 can mature according to two pathways depending on a given developmental function $J(j)$.

Within demographic heterogeneity, demographic stochasticity is at play as the chance realization of heterogeneous demographic parameters, or heterogeneous life cycle trajectories as in Figure 8.1m. Thus, demographic stochasticity is a component of demographic heterogeneity, but demographic heterogeneity also has an intrinsic component which can be deterministic or random, and is termed *individual heterogeneity*. Exploration of demographic heterogeneity is relatively recent, and the terminology is not yet standardized.

Demographic heterogeneity can be modeled by *individual based models* (IBM, Chapter 9). Insight is nevertheless gained from mathematical models (Box 8.5). A notable feature is that, under demographic heterogeneity, the relation between individual variation and population variation is complex: demographic variance may be either larger or smaller as compared to the corresponding homogeneous case (Kendall and Fox 2002, 2003; Vindenes et al. 2008). Individual heterogeneity is more likely to play a role in long-lived species than in short-lived species, where there is less correlation from one generation to the next.

Another insight is that more accurate models can be built when using total reproductive value instead of total population size (Engen et al. 2009). The *total reproductive value* at time t is calculated as $V(t) = \mathbf{v}\mathbf{n}(t) = \sum_i v_i n_i(t)$, where the reproductive value \mathbf{v} is normalized such that $\mathbf{v}\mathbf{w} = 1$. The metric is less sensitive than total population size N to fluctuations in population structure $\mathbf{w}(t)$ over time, and nevertheless verifies a similar relationship (Box 8.5):

$$\text{Var}(V(t+1)|V(t)=V) \approx \sigma_e^2 V^2 + \sigma_d^2 V. \quad (8.73)$$

The total reproductive value is the sum of individual reproductive values, which can be computed from individual data. *Environmental variance* σ_e^2 and *demographic variance* σ_d^2 can then be estimated. Fluctuations in population growth are affected by heterogeneity in individual reproductive values rather than heterogeneity in survival and reproduction.

A general framework is that, on top of the life cycle, individuals go along with their lives through a finite number of states with probabilities of switching between states given by a Markov matrix. The diversity of the individual trajectories or the successive states taken by an individual during its life reflects the demographic heterogeneity in the population.

Tuljapurkar et al. (2009) exemplify the case using capture-mark-recapture data with states corresponding to

offspring number. For example, if the states labeled 1, 2, 3, correspond to offspring number 0, 1–3, 4+, a possible individual trajectory is (1, 2, 2, 1, 3, ...). These authors quantify the degree of heterogeneity in the population (called *dynamic heterogeneity*) using the entropy of the Markov matrix.

Caswell (2009) built a Markov matrix \mathbf{u} from the stage-classified life cycle graph by removing reproductive arcs and incorporating an absorbing state corresponding to death. The states of this Markov chain are all transient, and probabilities to switch between states are given by the Markov matrix:

$$\mathbf{z} = \sum_{i=0}^{\infty} \mathbf{u}^i = (\mathbf{1} - \mathbf{u})^{-1}. \quad (8.74)$$

Sensitivities of demographic descriptors can be computed from the matrix \mathbf{z} to quantify demographic heterogeneity (called *individual stochasticity*).

Physiologically structured population models (PSPM, González-Suárez et al. 2011) work in a continuous-time continuous-state framework. The models rely on the bioenergetic mechanisms conditioning the vital rates, and allow us to finely track dynamics of cohorts, that is, sets of individuals born at the same time step, and to detect heterogeneous phenotypes in a population (Claessen et al. 2000).

8.9.1 Integral Projection Models

Some traits, like size, are best represented by continuous variables. Variations over time may follow smooth functions which can be parameterized using regression techniques. *Integral projection models* (IPM, Easterling et al. 2000; Ellner and Rees 2006, 2007; Briggs et al. 2010; Merow et al. 2014) use *continuous states* instead of the discrete stages or age-classes of matrix models. IPMs are good where sample sizes are small, or if discrete age- or size-classes are difficult to identify. They should sometimes be preferred to matrix models (Ramula et al. 2009). Projection equations analogous to Eq. (8.3) are obtained by summing over the space Ω of continuous states:

$$n(y, t+1) = \int_{\Omega} k(y, x) n(x, t) dx. \quad (8.75)$$

Here $n(x, t)$ is the distribution at time t of the number of individuals bearing the value (state) x of the trait. The kernel $k(y, x)$, which is an analogue of the projection matrix, can in practice be replaced by a large finite matrix. Integral projection models can also be used to account for demographic heterogeneity (Vindenes et al. 2011; Vindenes and Langangen 2015).

8.10 Software Tools

Matrix population analyses can be conducted with the `popbio` and `IPMpack` packages in Program R, or with general purpose programs for mathematical analyses such as Matlab or Mathematica. For this purpose of the online exercises, I demonstrate how matrix population modeling can be conducted with the ULM computer program (Legendre and Clobert 1995; Ferrière et al. 1996; Legendre 2008).

8.11 Online Exercises

The online exercises include example projection matrices for songbirds and wolves. Seven exercises illustrate models based on constant deterministic matrices, models with environmental stochasticity (with and without autocorrelation), a two-site model, and a two-sex model with demographic stochasticity.

8.12 Future Directions

I conclude by reviewing the main steps to construct a population dynamics model in a user-specific case. The principal advice is to keep the model as simple as possible, using the most basic assumptions, and analyzing different effects first separately, then in conjunction.

- 1) Construct the life cycle graph (Section 8.2) from what is known about the biology of the species of interest (life history, demographic parameter values), and according to the questions the biologist wants to answer concerning his case study. For unknown demographic rates, use data from the literature on a related species, or leave the entry as a parameter and explore several values (e.g. as in model file `wolf_0.ulm`). Here are examples of specific situations: Harvesting, poaching can be modeled by reducing appropriately the survival rates of the classes that are affected; Immigration, emigration, introductions can be dealt with by adding classes to the life cycle of the closed population (Figure 8.1j, Sarrazin and Legendre 2000). For uncertainty in demographic parameter values, or observation errors, see Morris and Doak (2002).
- 2) Build the associated matrix population model (Section 8.3.1) and compute the main demographic descriptors (growth rate, stable age distribution, reproductive value, generation time; Section 8.3.2).
- 3) Always perform a sensitivity analysis (Section 8.3.3). It provides insights into the demographic parameters that matter the most in the organism's life cycle (Box 8.2). Sensitivity analysis helps to determine the dynamical behavior when more complex dynamics

are introduced, such as density dependence, environmental stochasticity, and demographic stochasticity. Life-table Response Experiments (LTRE) are not discussed in this chapter, but can also be useful for decomposing the contributions of different demographic rates and their covariances to the overall variance of the population growth rate (Caswell 2001).

- 4) An alternative to matrix models is the use of IPMs for which there exists a convenient R package (`IPMpack`, Metcalf et al. 2013).
- 5) For small populations, say less than 100 individuals, it is recommended to introduce demographic stochasticity, and build two-sex models with a mating function. Two-sex models are necessary for the PVA of dimorphic species with mating systems that feature strong sexual selection (Section 8.8.2).
- 6) For metapopulations, spatial modeling comes into play (Section 8.7). Matrix models can be used as a first step toward more elaborate models of dispersion.
- 7) In many cases, an analysis based on a deterministic matrix model without variation in environmental conditions is enough to get a good idea of the demography of the studied population (Section 8.3). One must, however, recall that the constant matrix model mainly reveals potential short-term trends under a constant environment.
- 8) Density dependence requires the demographic data to be parameterized by a function, acting on the right classes and with the right parameters (Section 8.5). This is rarely met, but density dependence can be modeled for exploratory purposes with guessed parameter values.
- 9) Environmental stochasticity requires information on demographic parameter values over time, for example, in good and bad years (Section 8.6). Like density dependence, environmental stochasticity can be introduced for exploration, for example, to test the resilience of the species and get an estimate of its probability of extinction in an environment that is more realistic than the constant conditions assumed by the deterministic model (Section 8.3).

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