Appendix: From Stochastic Environments to Life Histories and Back

Shripad Tuljapurkar
Department of Biology
Stanford University
Stanford, CA 94305-5020, USA

Jean-Michel Gaillard
UMR 5558 Biometrie et Biologie Evolutive
Batiment G. Mendel
Université Claude Bernard Lyon 1
43 boulevard du 11 novembre 1918
69622 Villeurbanne Cedex, France

Tim Coulson
Department of Life Sciences
Imperial College London
Silwood Park, SL5 7PY, UK

Mathematical Formulas

We describe population change in discrete (annual) time steps using a matrix model. We consider only age-structured populations although many of our results can be generalized to stage-structured populations. Age classes are numbered 1 to k (actual ages are 0-1, 1-2, and so on). The population at census in year t is a vector $\mathbf{N}(t)$ of numbers in each age class and between t and $t+1$ the vital rates are contained in a $k \times k$ Leslie matrix $\mathbf{X}(t)$. We assume the environment is statistically stationary so that averages, covariances and serial covariances of the rates do not change with time.

Throughout we indicate averages (expectations) by $\mathcal{E}$. We denote the components of a matrix $\mathbf{H}$ by $H(i,j)$ and of a vector $\mathbf{u}$ by $u(i)$. The absolute value of a real or complex number z is denoted by $|z|$. Superscript T always indicates a transpose. The expression $(\mathbf{u}, \mathbf{v})$ denotes the scalar product of the vectors $\mathbf{u}$ and $\mathbf{v}$.

The average rates make up an average Leslie matrix $\mathbf{A}$ whose elements we call $a(i,j)$. Survivorship, R_0, T_c and σ_d are defined in the main text. The Lotka growth rate is $r = \log \lambda$ and $r \geq 0$ according as $R_0 \geq 0$ and vice versa.

We assume that $\mathbf{A}$ is a primitive irreducible matrix with dominant eigenvalue $\lambda = e^r$ and corresponding right, left eigenvectors $\mathbf{u}$, $\mathbf{v}$ respectively. These vectors are, respectively, the stable age structure and reproductive value (Caswell, 2001). Matrix $\mathbf{A}$ also has a subdominant eigenvalue

$$\lambda_1 = \exp(r_1 + is_1),$$

where r_1, s_1 are real numbers and $i = \sqrt{-1}$ so that $|\lambda_1| = \exp(r_1)$. In a population with average rates, a non-stable age distribution approaches $\mathbf{u}$ at a rate that increases with $(r - r_1)$. We say that the average life history is rapidly or slowly damped according as the speed of approach to stability is high or low.

We set $u(1) = v(1) = 1$ so that

$$u(i) = l(i) \, e^{-r(i-1)}, \text{ for all ages } i, \tag{1}$$

and

$$(\mathbf{v}, \mathbf{u}) = \sum_i i \, l(i) \, m(i) \, e^{-r \, i} = T = \text{Generation time in stable population.} \tag{2}$$

The matrix

$$\mathbf{Q} = \frac{\mathbf{A}}{\lambda} - \frac{\mathbf{u} \, \mathbf{v}^T}{\mathbf{v}^T \mathbf{u}}. \tag{3}$$

describes the transient behavior of the average demography. Fix the vital rates at their average values and change population structure away from the stable age distribution at $t = 0$: then the difference between population structure at time t and the stable structure is proportional to the powers $\mathbf{Q}^t \to 0$ as t increases. Consistent with our discussion of damping rates above, the magnitudes of the elements of $\mathbf{Q}^t$ go to zero at a rate $e^{(r_1 - r) \, t}$.

In year t the deviation of vital rates from their average values is denoted by $\mathbf{H}(t) = \mathbf{X}(t) - \mathbf{A}$. The within-year variance of matrix element $X(i, j, t)$ is denoted by

$$\sigma^2(i, j) = \mathcal{E}\left[H(i, j, t)\, H(i, j, t)\right] = \mathrm{Var}\left(X(i, j, t)\right). \tag{4}$$

The coefficient of variation of $X(i, j, t)$ is the ratio $(\sigma(i, j)/a(i, j))$.

The within-year covariance between the matrix elements $X(i, j, t)$ and $X(p, q, t)$ is denoted by

$$\mathrm{Cov}\,(ij, pq) = \mathcal{E}\left[H(p, q, t)\, H(i, j, t)\right] = \mathrm{Cov}\left(X(i, j, t)\, X(p, q, t)\right). \tag{5}$$

The within-year correlations between elements are defined by

$$\mathrm{Corr}(ij, pq) = \mathrm{Cov}(ij, pq)/(\sigma(i, j)\sigma(pq)). \tag{6}$$

The matrix element $X(i, j, t)$ may be correlated with its own future value $X(i, j, t + m)$ in year $(t + m), m > 0$ or with the future value $X(p, q, t + m)$ of some other matrix element. Statistical stationarity makes such correlations a function of only the lag m; we specify serial correlations in more detail below for our model life histories.

We consider populations that are growing slowly over the long run, meaning that the average fertility and mortality yield a growth rate r close to zero and the stochastic growth rate a is also close to zero. The former condition implies that the net reproductive rate R_0 is close to 1. In addition we assume that environmental fluctuations are small so that we can use the small-noise approximation for a (Tuljapurkar, 1982). As is well known (Morris and Doak, 2002; Lande et al., 2003) this approximation provides robust qualitative results for fairly large fluctuations.

The approximation for r in equation (7) of the main text is derived using a cumulant expansion (Keyfitz and Caswell, 2005). The sensitivities of $\lambda = e^r$ to the average rate are defined by

$$s(i, j) = \frac{\partial \lambda}{\partial a(i, j)} = \frac{v(i)u(j)}{T}. \tag{7}$$

Using these,

$$V_s = \frac{1}{2\lambda^2} \sum_{ij} s^2(i, j)\, \sigma^2(i, j), \tag{8}$$

$$V_c = \frac{1}{2\lambda^2} \sum_{(ij)\neq(pq)} s(i, j)\, s(p, q)\, \sigma(i, j)\, \sigma(p, q)\, \mathrm{Corr}(ij, pq). \tag{9}$$

The last term in equation (6) of the main text requires the matrix $\mathbf{Q}$ from equation (3) that describes transient dynamics, and correlations between vital rates at all time lags,

$$S = \frac{1}{\lambda^2 T}\, \mathbf{v}^T \left(\sum_{m=1}^{m=\infty} \mathcal{E}\left[\mathbf{H}(1 + m)\, \mathbf{Q}^m\, \mathbf{H}(1)\right] \right) \mathbf{u}. \tag{10}$$

2

References

H. Caswell. Matrix Population Models: Construction, Analysis, and Interpretation. *Sunderland, Massachusetts: Sinauer*, 2001.

N. Keyfitz and H. Caswell. *Applied Mathematical Demography*. Springer, 2005.

R. Lande, S. Engen, and B.E. Saether. *Stochastic populated dynamics in ecology and conservation*. Oxford University Press, 2003.

P. H. Leslie. The intrinsic rate of increase and the overlap of successive generations in a population of Guillemots (Uria aalge Pont.). *The Journal of animal ecology*, 35:291–301, 1966.

W.F. Morris and D.F. Doak. *Quantitative conservation biology Sinauer*. Sunderland, Massachusetts, USA, 2002.

S.D. Tuljapurkar. Population Dynamics in Variable Environments. III. Evolutionary Dynamics of r-Selection. *Theoretical Population Biology*, 21(1):141–165, 1982.