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Projection Matrices In Population Biology

Jan van Groenendael, Hans de Kroon and Hal Caswell

Projection matrix models are widely used in population biology to project the present state of a population into the future, either as an attempt to forecast population dynamics, or as a way to evaluate life history hypotheses. These models are flexible and mathematically relatively easy. They have been applied to a broad range of plants and animals. The asymptotic properties of projection matrices have clearly defined biological interpretations, and the analysis of the effects of perturbations on these asymptotic properties offers new possibilities for comparative life history analysis. The connection between projection matrix models and the secondary theorem of natural selection opens life cycle phenomena to evolutionary interpretation.

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Projection matrix models are an increasingly popular tool for describing population dynamics. They have been applied to a wide array of demographic problems (vegetative propagation¹, predator-prey interactions², competition³, two-sex populations⁴, weed control⁵, patch dynamics⁶, bud dynamics on trees⁷, density dependence⁸) for a variety of species ranging from mites² to whales⁹. Projection matrix models serve two main scientific purposes. First, they can be used in attempts to forecast population dynamics (e.g. of pest organisms^{2,10}). Second, because properties of the model correspond to life history characteristics such as fitness and reproductive value, they can be used to evaluate the long term consequences of hypothetical changes in the life cycle. Our review focuses on the latter application.

The simplest projection matrix models are discrete, linear, time invariant functions that map the

state of a structured population from one time to the next. The transition into the next state is assumed to depend only on the current state of the population. The entries in population projection matrix contain all necessary dynamical information, summarizing the ways in which survival, growth, development and reproduction change the composition of the population from one time to the next. In matrix notation this can be expressed as a simple multiplication:

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

Here \mathbf{n} is a state vector whose elements are the numbers of individuals in each recognized category, and \mathbf{A} is a square, non-negative matrix.

Part of the success of projection matrices is due to the flexibility of their mathematical formulation. One can choose almost any set of categories in which to classify individuals, any time step over which to evaluate transitions, and almost any complexity in transition pattern¹¹. Data from which to estimate the parameters of the model are at least conceptually straight-

forward to collect. One can also gradually add complexity to the system as needed, thus providing a hierarchical modelling approach².

Structuring the model

Size versus age

Population projection matrices were introduced into ecology by P.H. Leslie¹². His models were based on age intervals of the same duration as the time step in the model, which leads to a very specific structure of the matrix **A**, with age-specific fecundities F_i in the first row, age-specific survival probabilities P_i on the subdiagonal, and zeros elsewhere. A matrix with this form is commonly known as a Leslie matrix. However, when the demographic properties of individuals are not closely related to age, alternative classifications are needed. The categories into which individuals are classified should be defined so that transitions between categories are as unambiguous as possible. That is, categories should be chosen to minimize the uncertainty in the state of the population at time $t+1$, given the state at time

t . The choice of categories is thus one of the most important steps in developing a projection matrix model.

This problem was recognized 20 years ago, and projection matrices based on stage classification instead of age classifications were introduced by Lefkovich¹³. These matrices are more complex in appearance than the Leslie matrix because more transitions are generally possible between stages than between age categories, but their analysis is very similar.

Given a decomposition of the life cycle into categories (age classes, size classes, developmental stages, instars, or combinations of such categories), the transition structure of the life cycle can be shown with a life cycle graph (Fig. 1). The arrows in this graph indicate which transitions are possible for an individual from one time to the next; the coefficients on the arrows give the number of individuals produced at time $t+1$ per individual in the source category at time t . The projection matrix is obtained from the graph by inserting the coefficient

on the arrow from category j to category i in the (i,j) position in the matrix (Table 1).

The choice of stages in the description of the life cycle is strongly influenced by developmental patterns. For organisms with a markedly plastic development, it has been shown that stage categories are superior because demographic fate is more closely predictable from stage classes than from age categories^{11,14,15}. Most studies of mammals and birds, in which development is more deterministic, have used age categories. Age, however, may be important in addition to size, even in organisms with plastic development (Caswell, unpublished). For example, age and size have both been shown to be important in determining the growth and survival probability of reef corals¹⁶. Lacey¹⁷ lists several arguments why age-dependent reproduction contributes to the fitness of monocarpic plants, apart from or in interaction with size. The use of loglinear analysis to discriminate between age and size is presented by Caswell¹¹. When

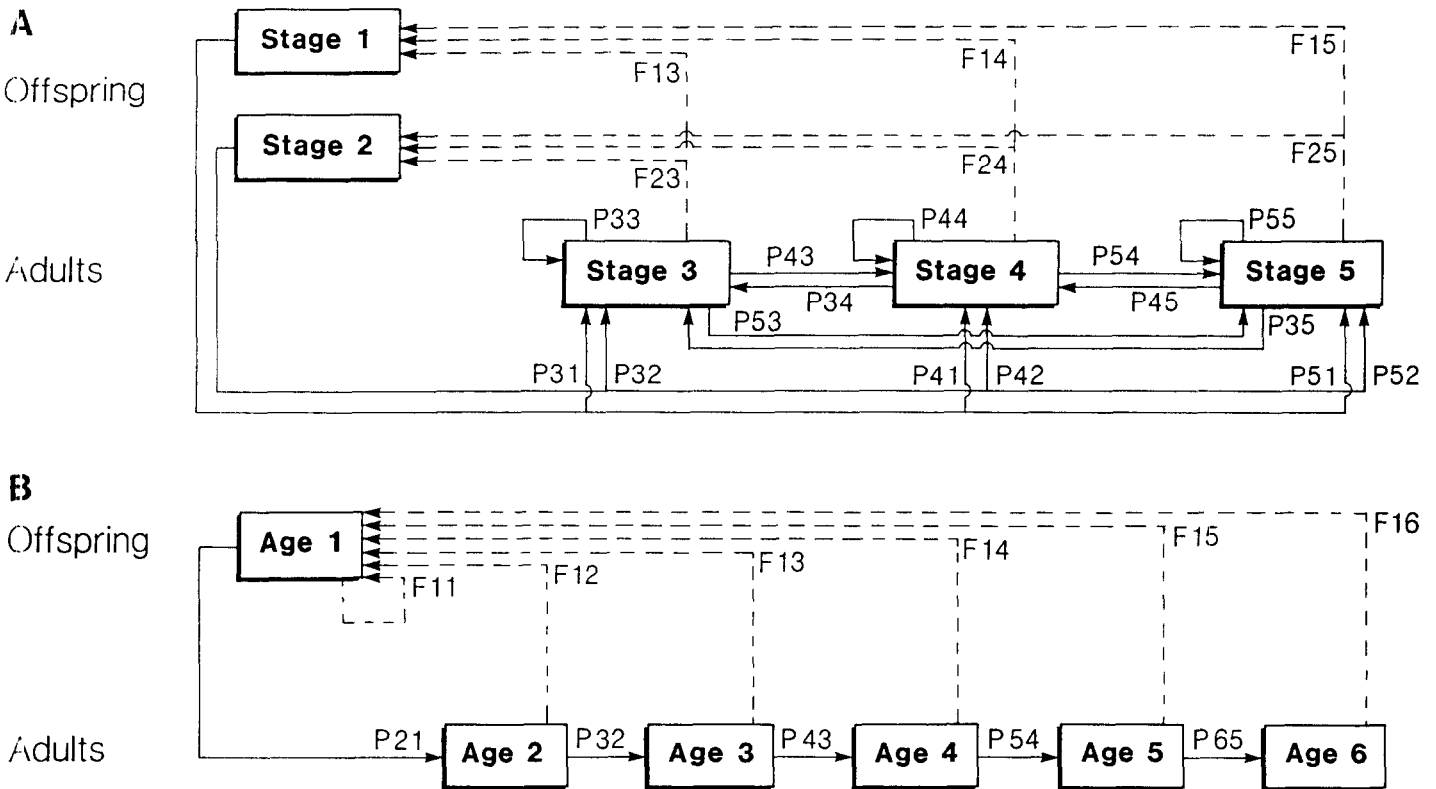


Fig. 1. Life cycle graphs for two contrasting life cycles, with survival probabilities (P) and recruitment (F) indicated. (A) Age-classified population of Plantain (*Plantago lanceolata*) (after Van Groenendael¹³). F_{11} indicates the possibility of producing seedlings from a seedbank. (B) Stage-classified population of Uinta ground squirrel (*Spermophilus armatus*) (after Sauer and Slade¹⁵). Offspring are produced in two size categories, denoted as Stage 1 and Stage 2.

Table 1. Projection matrices corresponding with the life cycle graphs of Fig. 1. (A) Leslie matrix for an age-classified Plantain population. (B) Size-classified matrix for the Uinta ground squirrel.

(A)

$$\begin{pmatrix} F_{11} & F_{12} & F_{13} & F_{14} & F_{15} & F_{16} \\ P_{21} & - & - & - & - & - \\ - & P_{32} & - & - & - & - \\ - & - & P_{43} & - & - & - \\ - & - & - & P_{54} & - & - \\ - & - & - & - & P_{65} & - \end{pmatrix}$$

(B)

$$\begin{pmatrix} - & - & F_{13} & F_{14} & F_{15} \\ - & - & F_{23} & F_{24} & F_{25} \\ P_{31} & P_{32} & P_{33} & P_{34} & P_{35} \\ P_{41} & P_{42} & P_{43} & P_{44} & P_{45} \\ P_{51} & P_{52} & P_{53} & P_{54} & P_{55} \end{pmatrix}$$

significant interactions are present between age and size, then a two-dimensional model using age and size simultaneously is an appropriate tool^{18,19}.

Number of categories

In addition to choosing which categories to use, one must also choose an appropriate number of categories²⁰. Too many categories reduces the accuracy of parameter estimation, because sample sizes in each category become smaller, while too few categories give too little resolution of demographic processes. In addition, the distribution of individuals among categories is usually skewed in natural populations, with an over-representation of the young (small) categories and an under-representation in the older (larger) categories. This calls for an appropriate (log) transformation before establishing the number of categories. The choice of the number of categories can be optimized using the algorithm proposed by Moloney²⁰.

Time steps

To be widely applicable, projection matrix models must overcome some of the shortcomings of a model with discrete time steps. The choice of time step over which to evaluate the transition probabilities in the model is crucial. In this connection, the distinction between populations with continuous and discrete reproduction ('birth-flow' or 'birth-pulse' populations²¹) is important. In birth-pulse populations, it is important to know where these pulses are located with respect to the time step, because this determines the correct formulae for the projection matrix elements (Caswell, unpublished). The fecundity terms in particular must include the risk of offspring mortality between birth and the time when they are counted as part of the population. Mature individuals also have a probability of dying after being counted, but before reproducing; this must be taken into account. In birth-flow populations, the solution to these problems¹² involves integrating continuous mortality and fertility functions over the time interval (De Roos, unpublished; Caswell, unpublished).

The choice of the time step is also related to the time scale of environmental variation. Difficulties arise when the time step in the model is longer than the time scale of the relevant environmental variation. A way around this problem is to increase the number of time steps, so as to achieve a finer picture in time^{5,10}. However, this may introduce delayed responses, in which the demographic effects of an event do not show up in the next time step but one or more time steps later. An example of handling several time delays together is presented by Paton¹⁰, in his modelling of a nematode parasite in the intestines of sheep.

Historical effects

Relatively little work has been done on historical effects, or time-lags, in projection matrices. Such effects can be expressed as follows:

$$\mathbf{n}(t+1) = \mathbf{A}[\mathbf{n}(t-x) | \mathbf{n}(t)], \quad (2)$$

with $x \geq 1$. Here, the projection matrix $\mathbf{A}[\mathbf{n}(t-x) | \mathbf{n}(t)]$ explicitly depends on the previous state of the

population. Such historical effects are likely in natural populations and have been demonstrated in some cases^{2,22}. For example, a small, newly established colony of a reef coral¹⁶ has a much larger survival probability than an older, senescent, colony of the same size. In a model based only on size, this difference would appear as a historical effect. One solution, of course, would be to increase the numbers of categories by constructing a new model distinguishing ages within size categories. In theory all historical effects can be incorporated in this way, but in practice this may be impractical. To what extent historical effects influence the results of the analysis of projection matrices remains to be investigated.

Analysing the model

Limit properties

Provided certain technical conditions are met (see Caswell¹¹ for review) the population dynamics produced by continued iteration of Equation (1) converge to a stable population structure, independent of the initial conditions. This stable population grows (or declines) at a constant rate λ .

These important asymptotic properties, as well as the reproductive value distribution, are obtained directly from the eigenvalues and eigenvectors (see Box 1) of the projection matrix, which can be calculated either numerically or analytically. Their demographic interpretation is given in Box 2.

These demographic limit properties have been used to compare species, or populations of the same species (e.g. Refs 14, 15, 19, 23) and can also be used to evaluate the results of a conceptually limitless number of Kantian thought experiments ('what if...' questions). In such experiments, the model is used to project the consequences of a certain constellation of demographic parameters. Useful insight can often be obtained from examining the effects of hypothetical life history changes, even when the changes are known to be unrealistic. This use of the model is very different from the population forecasts with which these projections are often confused. The aim of a projection is not to forecast accurately the future state of the popu-

Box 1. Eigenvalues and eigenvectors

A vector \mathbf{x} is a right eigenvector of a matrix \mathbf{A} if

$$\mathbf{Ax} = \lambda \mathbf{x} \quad (1)$$

for some $\lambda \neq 0$; λ is the corresponding eigenvalue. A vector \mathbf{y} is a left eigenvector of \mathbf{A} if

$$\mathbf{y}'\mathbf{A} = \lambda \mathbf{y}' \quad (2)$$

for some $\lambda \neq 0$. That is, the eigenvectors of a matrix are vectors for which multiplication by the matrix is equivalent to multiplication by a scalar factor. The eigenvalues are those scalar factors.

lation, but to examine the ultimate consequences of the present state and the structure of the life cycle, should everything remain the same¹¹. This projection technique is a powerful tool and its possibilities to generate testable hypotheses are not yet fully exploited.

This does not imply that projection models cannot be used for short-term prediction or forecasting (e.g. Ref. 2), but asymptotic properties like λ , which apply in the limit as $t \rightarrow \infty$, are unlikely to be of great use in such forecasts.

Perturbation analyses

The limit properties of projection matrices have the great advantage of summarizing the complex demographic information contained in the life cycle diagram into a few summary statistics (λ , \mathbf{w} , \mathbf{v}). This is also their weakness, however, because this summary obscures the effect of the separate matrix elements (or life history components¹⁴). Perturbation analysis extends the Kantian thought experiment by helping to untangle the influence of age- or stage-specific traits on the asymptotic properties of the population.

Consider the population growth rate λ (see Caswell¹¹ for the perturbation analysis of other limit properties). This rate is a function of all the entries a_{ij} of the projection matrix \mathbf{A} . Changes in any of these entries will change λ . The question addressed by perturbation analysis is, how sensitive is λ to a small change in each of the a_{ij} , holding all others constant? Define s_{ij} as the sensitivity of λ to a change in a_{ij} . Caswell²⁴ showed that this sensitivity can be calculated directly from the eigenvectors of \mathbf{A} :

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_j w_i}{(\mathbf{w}, \mathbf{v})} \quad (3)$$

where w_j is the j^{th} element of the right eigenvector (stable stage distribution) \mathbf{w} , v_i is the i^{th} element of the left eigenvector (reproductive value) \mathbf{v} , and (\mathbf{w}, \mathbf{v}) denotes the scalar product.

Evaluating this sensitivity for all the entries in the matrix \mathbf{A} produces a new matrix \mathbf{S} containing the sensitivities of the population growth

Box 2. The demographic interpretation of various algebraical properties of population projection matrices

Symbol	Name	Definition
\mathbf{A}	Population projection matrix	A square matrix containing coefficients representing rates of survival, reproduction, growth, development, maturation, movement, etc.
a_{ij}	Matrix element	The entry in row i , column j of the projection matrix \mathbf{A} .
λ	Population growth rate	The largest of the eigenvalues of the projection matrix \mathbf{A} .
\mathbf{w}	Stable stage distribution	The right eigenvector of \mathbf{A} corresponding to λ .
\mathbf{v}	Reproductive value distribution	The left eigenvector of \mathbf{A} corresponding to λ .
(\mathbf{w}, \mathbf{v})	Scalar product	$\sum_i v_i w_i$
s_{ij}	Growth rate sensitivity	The sensitivity of λ to changes in the matrix element a_{ij} , given by $\partial \lambda / \partial a_{ij}$.
e_{ij}	Growth rate elasticity	The proportional sensitivity of λ to a proportional change in the matrix element a_{ij} .

rate to shifts in all the elements of \mathbf{A} . This opens the possibility of comparing the importance of various matrix elements (or life history components) for the population under study.

The sensitivities s_{ij} measure the absolute sensitivity of λ to absolute changes in the matrix elements a_{ij} . Because projection matrices combine fecundity terms and survival terms, which are usually measured on different scales, it is often biologically interesting to examine the *proportional effect of proportional changes* in the matrix elements. Such proportional sensitivities have often been calculated in numerical perturbation calculations²⁵, by simply changing each matrix element by a given percentage (e.g. 10%). However, the proportional sensitivities (or *elasticities*, adopting the usage of the term in microeconomics) can also be calculated directly from the projection matrix²⁶:

$$e_{ij} = \frac{\partial \ln \lambda}{\partial \ln a_{ij}} = \frac{a_{ij} \partial \lambda}{\lambda \partial a_{ij}} \quad (4)$$

De Kroon *et al.*²⁶ have shown that the e_{ij} always sum to unity. They thus represent the relative contribution of each element to the population growth rate (Table 2). They can be used to compare the importance of demographic parameters among species, among dif-

ferent populations within a species, and among different pathways within the life cycle (e.g. sexual vs asexual reproduction or growth vs reproduction^{26,27}).

Linearity

So far we have considered only the simplest linear, deterministic, time invariant projection matrices. Now we want to discuss what happens when we relax these assumptions, one at a time. Non-linear

Table 2. Elasticity matrices for (A) an age-classified population (Plantain – Fig. 1A, Table 1A), and (B) a stage-classified population (Uinta ground squirrel – Fig. 1B, Table 1B).

(A)							
Age	1	2	3	4	5	6	Sum
1	.019	.148	.115	.042	.024	.009	.357
2	.337	–	–	–	–	–	.337
3	–	.189	–	–	–	–	.189
4	–	–	.075	–	–	–	.075
5	–	–	–	.033	–	–	.033
6	–	–	–	–	.009	–	.009
sum	.356	.337	.190	.075	.033	.009	1.000

(B)						
Stage	1	2	3	4	5	Sum
1	–	–	.064	.108	.077	.249
2	–	–	.010	.037	.046	.093
3	.099	.031	.015	.001	.000	.146
4	.117	.049	.045	.064	.025	.300
5	.033	.013	.013	.088	.067	.214
Sum	.249	.093	.147	.298	.215	1.002

Population growth rates are 1.84 and 0.97 respectively. Note that elasticities sum to unity in both cases (except for rounding errors).

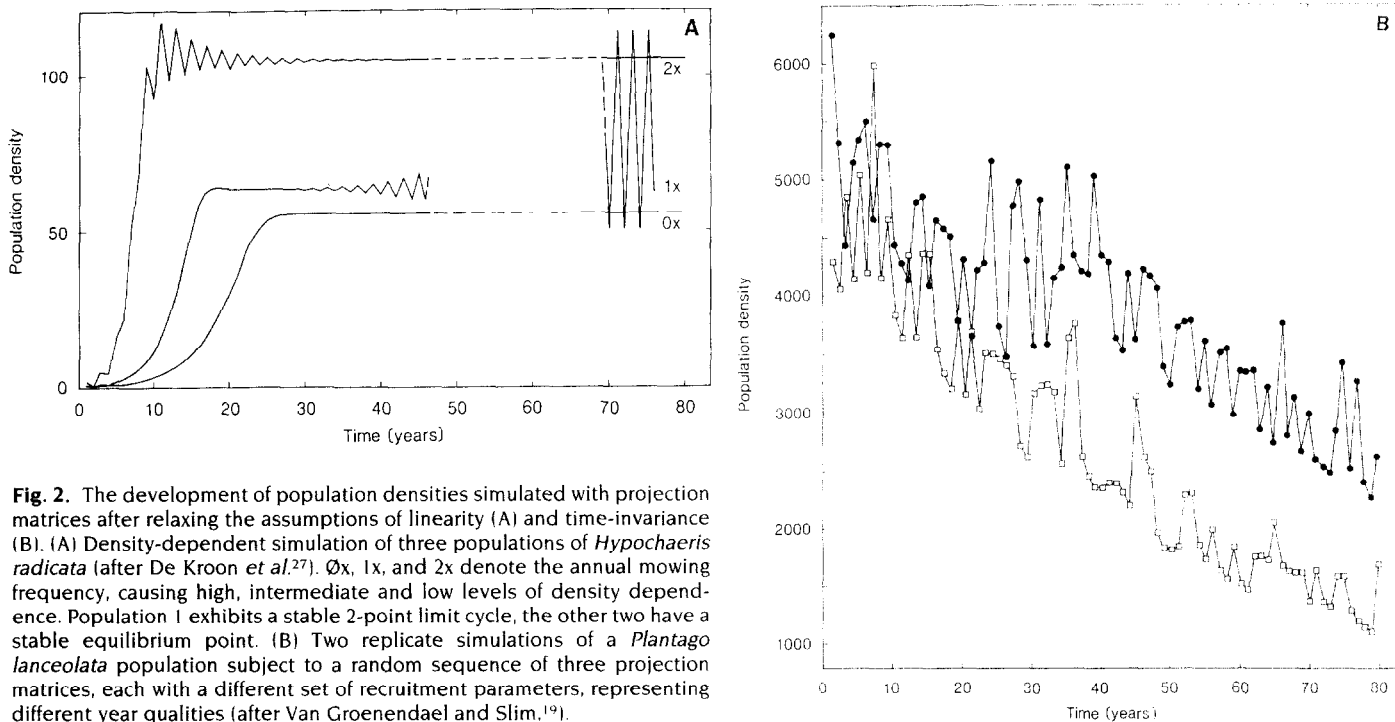


Fig. 2. The development of population densities simulated with projection matrices after relaxing the assumptions of linearity (A) and time-invariance (B). (A) Density-dependent simulation of three populations of *Hypochaeris radicata* (after De Kroon *et al.*²⁷). 0x, 1x, and 2x denote the annual mowing frequency, causing high, intermediate and low levels of density dependence. Population 1 exhibits a stable 2-point limit cycle, the other two have a stable equilibrium point. (B) Two replicate simulations of a *Plantago lanceolata* population subject to a random sequence of three projection matrices, each with a different set of recruitment parameters, representing different year qualities (after Van Groenendael and Slim.¹⁹).

projection matrices arise when feedback mechanisms cause the entries of the projection matrix to be functions of the state vector **n**. In matrix formulation this is expressed

as follows:

$$\mathbf{n}(t+1) = \mathbf{A}[\mathbf{n}(t)] \mathbf{n}(t) \quad (5)$$

Such feedback mechanisms may depend on the absolute values in the state vector **n** (density dependence) or on their relative proportions (frequency dependence). The latter case is important in two-sex models, in which relative abundance of males and females determines reproductive output⁴.

The most frequently considered feedback mechanism is density dependence (e.g. Refs 8, 9, 27 and many others). One, several or all of the matrix elements are written as functions of density. This density function frequently takes the form of an exponential decrease in a_{ij} as density increases, although sometimes a sigmoid function is used⁹, producing greatest density effects at intermediate levels.

Non-linear projection matrices rapidly become analytically intractable. In most cases, they have been studied numerically, applying iteration techniques^{27,28}, although their local stability analysis is now well understood²⁸. When the equilibrium is unstable, complex dynamic behavior, including series of bifurcations leading to chaos, can result²⁸ (Fig. 2).

Time invariance

Demographic parameters are well known to vary over time. This affects the elements of the projec-

tion matrix, and can be expressed as:

$$\mathbf{n}(t+1) = \mathbf{A}(t)\mathbf{n}(t) \quad (6)$$

The function **A**(*t*) is not usually known explicitly, and in practice the solution has been to apply a series of matrices to accommodate the differences over time. Differences may occur between years²⁹, between seasons²⁷, or within one season^{2,5}. Random combinations of different projection matrices have been used to simulate stochastic temporal variability^{10,19,29} (see Fig. 2). This relates to a body of theoretical work exploring the behavior of projection matrices and their limit properties, when the matrix elements are stochastic variables^{30,31,32}. These studies show the dramatic effects of stochastic variation on the asymptotic properties of projection matrices and the need to modify the concepts of population growth rate³³ and its sensitivity³¹ in predicting the fate of a population in a stochastic environment. The consequences of these findings have as yet not been fully incorporated in life history studies, but a few preliminary attempts have been made³³, testing the consequences of variation in development rate on long term growth rate.

Evolutionary interpretation of the model

One of the more exciting aspects of matrix projection models is the

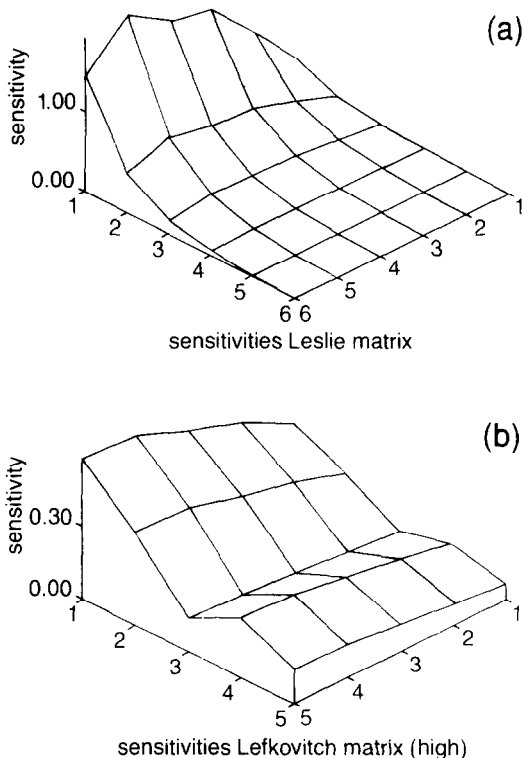


Fig. 3. Sensitivities for two contrasting projection matrices, (a) a Leslie matrix for Plantain (Fig. 1A, Table 1A), and (b) a size-classified matrix for the Uinta ground squirrel (Fig. 1B, Table 1B). The axes correspond to the rows (*i*) and columns (*j*) of the corresponding projection matrices. Note the generally similar shifts in sensitivities, decreasing in the matrix from left to right and from back to front, in both populations, apart from species-specific differences in magnitude and slope.

possibility of linking them with quantitative genetic theory. This lifts these models from a largely descriptive tool or forecasting aid into the more speculative realm of evolutionary theory. This link is most clearly stated in Lande's³⁴ version of the Secondary Theorem of Natural Selection. This theorem describes the rate of change in the phenotypic mean of a set of traits:

$$\Delta \bar{z} = \lambda^{-1} \mathbf{G} \nabla \lambda \quad (7)$$

where \mathbf{z} is a vector of phenotypic means, \mathbf{G} is the additive genetic covariance matrix for these traits, and $\nabla \lambda$ is a vector of selection gradients on the traits,

$$\nabla \lambda = \begin{bmatrix} \frac{\partial \lambda}{\partial \bar{z}_1} \\ \frac{\partial \lambda}{\partial \bar{z}_2} \\ \vdots \\ \frac{\partial \lambda}{\partial \bar{z}_k} \end{bmatrix} \quad (8)$$

These selection gradients are precisely the eigenvalue sensitivities discussed earlier. Those sensitivities, which can be calculated directly from the projection matrix, thus give the direction and the intensity of selection on the life history characteristics of the organism^{1,35}.

When the sensitivity matrix \mathbf{S} is calculated, the results almost always indicate an increase in sensitivity towards the left upper and lower corner elements of the matrix (Fig. 3). In an evolutionary context this indicates that it is always profitable to reproduce early and to grow fast. This is an obvious solution, but equally obviously, evolution has not moulded all life histories in this direction. The explanation lies in the fact that life history traits are not free to vary independently^{36,37}. In genetic terms, this lack of independence is expressed in the genetic covariance matrix \mathbf{G} ; in life history theory it appears in the form of hypotheses about 'constraints', 'trade-offs', 'costs of reproduction', etc. A fruitful approach is to formulate trade-offs between various life history traits and to analyse the shifts in population growth rate as a result of shifts in the respective traits over

the trajectory described by the trade-off function¹. This approach has produced testable hypotheses on, e.g. sexual and clonal reproduction¹, senescence^{1,24}, dormancy and plasticity³⁸. There are now good opportunities to develop actual trade-offs based on genetic covariances³⁶, rather than formulating hypotheses about these trade-off functions. The choice of trade-off should be based on morphological, physiological and/or genetical constraints, which are most likely to play a role in the life history changes under study.

It is important to note that this evolutionary interpretation is based on the simplest deterministic linear model. The implications of relaxing these restrictions are only beginning to be studied. Particularly important are non-stable age/size distributions, stochasticity, and density/frequency dependence. Many authors have called for a closer cooperation between population biologists and population geneticists³⁹; matrix projection models, applied in an evolutionary context, could provide a tool to bridge this gap. Future developments in this direction may be very promising.

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