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Matrix models

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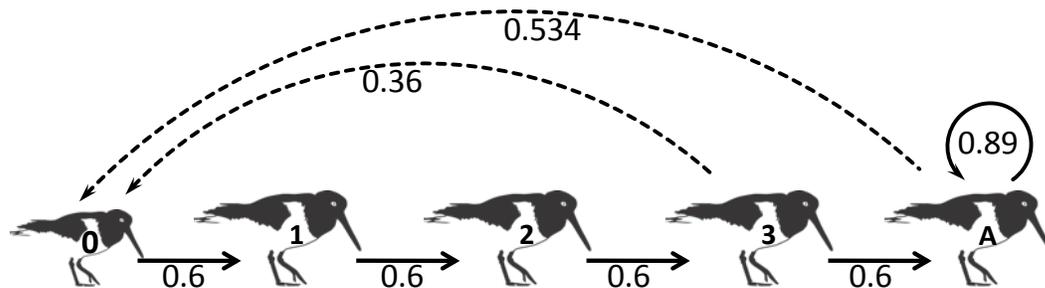
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Transition matrix population models quantify all ways (through survival and reproduction) in which individuals contribute to the size of the population after one time step. Matrix models thus represent the life cycle of individuals, and can be used to investigate the dynamics of a population. Several analytical characteristics of transition matrices have clear biological interpretations, making matrix models simple and insightful models for fundamental and applied population studies.

I. The concept

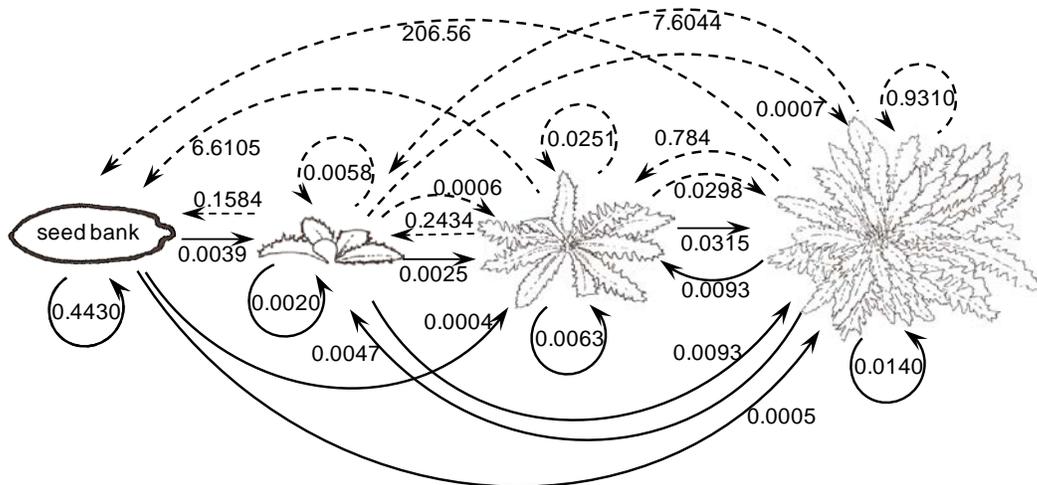
Individual plants and animals are born, survive until a certain age, meanwhile change in size and appearance, and may reproduce sexually and/or asexually. Together with migration these demographic processes determine whether local populations of individuals grow or decline in number. Quantifying all involved demographic rates therefore allows a researcher to study the dynamics of population size through time. Models of population dynamics can not only be used to answer fundamental questions like ‘which demographic process contributes most to population growth?’, but also to important applied questions like ‘how effective will various management options be to control an invasive population?’ or ‘how likely is a population of an endangered species to go extinct over time?’ At first such fundamental and applied questions were tackled by summarizing the fate (e.g. survival and number of offspring) of cohorts of individuals in tables or flow charts. Later the important step was made from flow charts to life cycle graphs and transition matrix population models.

Transition matrices contain exactly the same information as life cycle graphs, but then organized in matrix form. The two life cycle examples in Figures 1 and 2 thus illustrate the basic idea of matrix models. The purpose is to bring together all demographic processes at a location (migration is often ignored). The first thing to note in these examples is that individuals are classified in different groups, based on e.g. their age, developmental stage, or size. The second thing to note are the arrows between these classes of individuals. Each arrow represents the contribution of an average individual in one class to the number of individuals in a particular class one time step later. Often this time step is 1 year (as assumed in the remainder of this chapter), but other transition periods are possible as well. There are two ways in which an individual can contribute to the number of individuals in the next year: either through surviving (solid arrows; including age and size changes) or through reproducing (dashed arrows).



$$\begin{pmatrix} fledglings_{t+1} \\ one_{t+1} \\ two_{t+1} \\ three_{t+1} \\ adults_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0.36 & 0.534 \\ 0.6 & 0 & 0 & 0 & 0 \\ 0 & 0.6 & 0 & 0 & 0 \\ 0 & 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0 & 0.6 & 0.89 \end{pmatrix} \begin{pmatrix} fledglings_t \\ one_t \\ two_t \\ three_t \\ adults_t \end{pmatrix}$$

Figure 1. Life cycle graph and corresponding transition matrix of an Oystercatcher (*Haematopus ostralegus*) population in Wales, with post-breeding census and age-based classes (C. Klok et al. 2009 Anim. Biol. 59:127-144; drawings by N. Roodbergen). Only females are modeled. The solid arrows and accompanying numbers are annual survival rates, whereas the dashed arrows represent the average number of fledglings produced after one year. The projected population growth rate (λ) is 0.974, meaning that the population is projected to decline with 2.6% per year if these model parameters remain unchanged



$$\begin{pmatrix} seedbank_{t+1} \\ small_{t+1} \\ medium_{t+1} \\ large_{t+1} \end{pmatrix} = \begin{pmatrix} 0.4430 + 0 & 0 + 0.1584 & 0 + 6.6105 & 0 + 206.56 \\ 0.0039 + 0 & 0.0020 + 0.0058 & 0.0000 + 0.2434 & 0.0047 + 7.6044 \\ 0.0004 + 0 & 0.0025 + 0.0006 & 0.0063 + 0.0251 & 0.0093 + 0.7837 \\ 0.0005 + 0 & 0.0093 + 0.0007 & 0.0315 + 0.0298 & 0.0140 + 0.9310 \end{pmatrix} \begin{pmatrix} seedbank_t \\ small_t \\ medium_t \\ large_t \end{pmatrix}$$

Figure 2. Life cycle graph and corresponding transition matrix of a Nodding Thistle (*Carduus nutans*) population in Australia, with post-breeding census and stage classification based on developmental stage (seed or rosette) and rosette size (K. Shea et al. 2010 Ecol. Appl. 20:1148-1161). The solid arrows represent survival/growth and the accompanying rates give the proportion of individuals that survive and move to a particular class. The dashed arrows involve production (via seed) of new individuals after one year. The elements of the accompanying 4x4 matrix model are often a sum of a survival transition and a reproduction contribution. The projected population growth rate (λ) is 1.207 (based on the rounded matrix elements shown here), projecting an increase in population size of 20.7% per year

Once all transition arrows are quantified, and if you know the initial number of individuals in each class, you can calculate the population size after one time step by multiplying each arrow with its corresponding initial group size. This multiplication can be made easier by rearranging

the transition arrows into a matrix, as is done in Figures 1 and 2. In a matrix the transition rates are arranged such that a column contains all contributions *by* an average individual in a particular class, while a row contains all contributions *towards* the number of individuals in a particular class after one time step. Multiplication of the transition matrix with a vector of the initial number of individuals per class, immediately results in the population vector after 1 time step:

$$\begin{pmatrix} \text{fledglings}_{t+1} \\ \text{one}_{t+1} \\ \text{two}_{t+1} \\ \text{three}_{t+1} \\ \text{adults}_{t+1} \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & 0.36 & 0.534 \\ 0.6 & 0 & 0 & 0 & 0 \\ 0 & 0.6 & 0 & 0 & 0 \\ 0 & 0 & 0.6 & 0 & 0 \\ 0 & 0 & 0 & 0.6 & 0.89 \end{pmatrix} \begin{pmatrix} 100 \\ 200 \\ 300 \\ 400 \\ 500 \end{pmatrix} = \begin{pmatrix} 0.36 * 400 + 0.534 * 500 \\ 0.6 * 100 \\ 0.6 * 200 \\ 0.6 * 300 \\ 0.6 * 400 + 0.89 * 500 \end{pmatrix} = \begin{pmatrix} 411 \\ 60 \\ 120 \\ 180 \\ 685 \end{pmatrix}$$

If the initial population size was 1500 birds (including 100 fledglings and 500 adults), the transition matrix projects 1456 birds after one year. Multiplication of the population vector with the same transition matrix for ten successive time steps results in Figure 3.

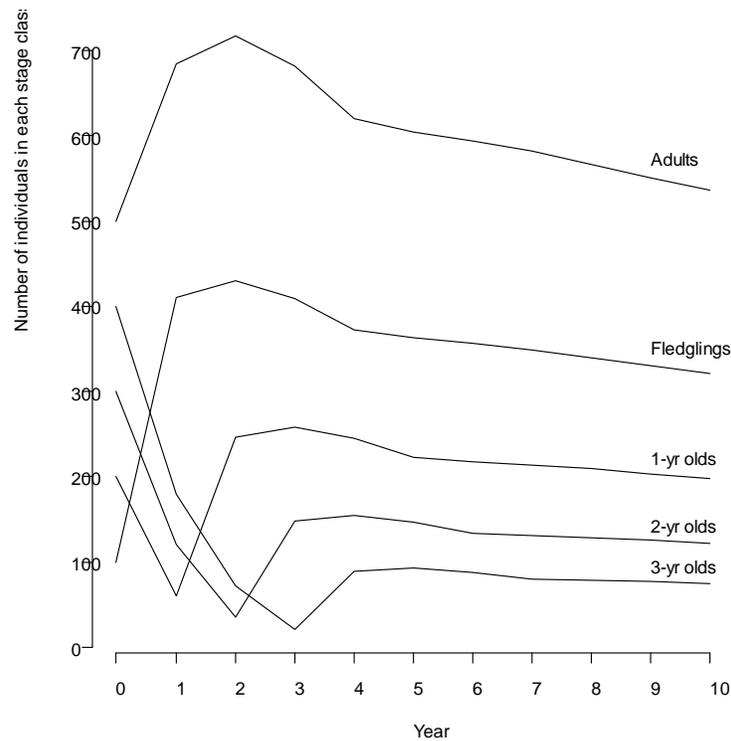


Figure 3. Trajectory of the number of Oystercatchers in each of the five age classes over ten years. The initial population in year 0 consisted of 100 fledglings, 200 1-yr olds, 300 2-yr olds, 400 3-yr olds and 500 adults. Each time step the population vector was multiplied by the transition matrix depicted in Fig. 1. After some years with transient dynamics the distribution of the number of birds over the classes stabilizes: eventually both the total population size and the number of individuals in each class declines by the same factor $\lambda=0.974$.

Transition matrices are not only useful for matrix-vector multiplication but also because matrix algebra can be applied. Many of the analytical properties of matrices have clear biological

meaning. One of these, the dominant ‘eigenvalue’ of a matrix for instance gives the asymptotic growth rate of a population (see Box 1). This is the per capita growth rate that is eventually reached when the same transition matrix is used over many time steps to project what will happen to population size in the long run. In population studies the projected population growth rate is often symbolized by λ , and λ values above 1 indicate that a population will increase in size if the demographic rates in the transition matrix remain the same. Values of λ between 0 and 1 signal decreases in population size, as with the Oystercatcher example in Fig. 1.

Not only the proportional increase (or decrease) in population size reaches an asymptotic value after repeatedly multiplying the same matrix many times to a population vector. The ratios between the number of individuals in the various classes also become fixed (see Fig. 3): all these numbers eventually also change by a factor λ each time step. The asymptotically fixed proportions of the total population size in each of the classes are called the ‘stable stage distribution’ and is given analytically by the right eigenvector (another property of the transition matrix) that corresponds to the dominant eigenvalue (see Box 1). The left eigenvector is also informative: it gives the reproductive values for each of the classes, i.e. the number of offspring produced during the life time of an average individual starting in that class.

II. Model parameterization

How do you parameterize a matrix model from your raw demographic field data? First you have to decide whether you want to classify individuals by age or by some other classification based on e.g. age, size, developmental or reproductive status. Other important decisions are whether all individuals are included in the model (or e.g. only females as in the Oystercatcher model), and at what time of the year the population is censused. The latter is important for the stage classification as in a post-breeding census new-born individuals can be a class, whereas in a pre-breeding census the youngest individuals are almost 1 year old already.

In age-based matrices in which the individuals move up one class every time step, survival and growth are indistinguishable and entered in the subdiagonal of the matrix (Fig. 1). Often, as in the Oystercatcher example, age-specific classes are combined with age-based stage classes like ‘Adults’ in which individuals above a certain age are pooled. When classification is based on size as in the Nodding Thistle example, many more transitions between stages are possible (Fig. 2). These represent life histories in which it is possible for individuals to skip classes, remain in the same class (‘stasis’), or regress to a previous class (e.g. shrinkage in plants). The non-reproductive elements of these matrices can be seen as products of two so-called vital rates: first the survival rate of individuals in a class until the next census (irrespective of the classes to which individuals move) and second the ‘growth’ rates: next-year’s distribution of individuals from a class over all classes in the model (conditional to survival).

When calculating reproduction rates it is important to remember the time step of the model: how many new offspring are alive one year later per average individual in a class now. The estimation of reproduction matrix elements therefore often involves multiplying different vital rates. In the Oystercatcher model the reproduction matrix elements consist of the product of the survival probability of a bird until the next year, and the average number of (female) fledglings per surviving bird. The order and time span of these vital rates also depend on the choice of the census moment (e.g. after the reproduction pulse like in the Oystercatcher and Nodding Thistle

Box 1.

Eigenvalues and eigenvectors are characteristic properties of transition matrix. Here we will give a short explanation of how these can be found for a simple 2x2 transition matrix:

$$A = \begin{pmatrix} 0.1 & 2 \\ 0.3 & 0.5 \end{pmatrix}$$

As seen in Fig. 3, when the population vector is multiplied with the same transition matrix each time step, any initial population will eventually grow in size with a certain asymptotic population growth rate. This asymptotic population growth rate is equal to the dominant eigenvalue (λ) of the transition matrix. The right eigenvectors (w) associated with the dominant eigenvalue are population vectors of which the proportional distribution of individuals over the stage classes does not change after multiplication with the transition matrix, e.g.:

$$\begin{pmatrix} 0.1 & 2 \\ 0.3 & 0.5 \end{pmatrix} \begin{pmatrix} 20 \\ 10 \end{pmatrix} = \begin{pmatrix} 0.1 * 20 + 2 * 10 \\ 0.3 * 20 + 0.5 * 10 \end{pmatrix} = \begin{pmatrix} 22 \\ 11 \end{pmatrix}$$

This 67%:33% distribution of the individuals over the two stage classes was the same before and after the matrix multiplication, and is called the 'stable stage distribution'. We can also see that λ must be 1.1. But how can we derive these dominant eigenvalues and eigenvectors? The first thing to realize is that for a population with a 'stable' structure multiplication with transition matrix A gives the same result as multiplication with λ , the asymptotic population growth rate: $Aw = \lambda w$. We can rewrite this as $Aw - \lambda w = 0$ or $(A - \lambda I)w = 0$, where I is an identity matrix with ones on the diagonal and zeros elsewhere. This set of linear equations can be solved for λ by using the determinant: $\det(A - \lambda I) = 0$. For our example this works out as follows:

$$\det \left(\begin{pmatrix} 0.1 & 2 \\ 0.3 & 0.5 \end{pmatrix} - \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix} \right) = 0$$

$$\det \begin{pmatrix} 0.1 - \lambda & 2 \\ 0.3 & 0.5 - \lambda \end{pmatrix} = 0$$

$$(0.1 - \lambda)(0.5 - \lambda) - (0.3)(2) = 0$$

$$\lambda^2 - 0.6\lambda - 0.55 = 0$$

Of the solutions for λ , -0.5 and 1.1, the latter has the highest absolute value and will determine the asymptotic population growth rate. The stable stage distribution (w) can now be found by substituting $\lambda = 1.1$ in $(A - \lambda I)w = 0$:

$$\begin{pmatrix} 0.1 - 1.1 & 2 \\ 0.3 & 0.5 - 1.1 \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Suppose that n_2 is 1, then the second equation becomes $0.3n_1 - 0.6 = 0$ leading to $n_1 = 2$. This shows that the stable ratio $n_1:n_2$ is 2:1 or 67%:33%.

Such matrix calculations become increasingly complex with larger matrix dimension, but can easily be done with mathematics-oriented software packages (e.g. Matlab). However, most calculations can also be done with e.g. the PopTools add-in in Excel, or with the popbio package in R.

cases). In some cases it might also be possible to produce different types of offspring, e.g. small versus large seedlings, or sexually versus asexually produced offspring.

Because each matrix model represents a species- or even population-specific life history, and because of different model construction choices made by researchers, it can be hard to compare models between studies. Attempts have therefore been made to categorize matrix elements into groups representing e.g. reproduction, survival and growth. The problem, however, with such matrix element classifications is that the non-reproductive elements in a column are not independent: their sum is bound between 0 and 1 (i.e. between 0% and 100% survival) as in the first column of the thistle model: when a high proportion of seeds in the seed bank remain dormant, the transition rates from the seed bank to the rosette stages cannot be very high. For comparative demography it is therefore more useful to focus on the vital rates that were used to construct the matrix elements. The survival and growth rates described in the previous paragraphs do vary independent of each other. An additional advantage of analyses at the level of vital rates is that these vital rates have clearer biological meaning than matrix elements that are often constructs of multiple vital rates.

III. Sensitivity and Elasticity

Once you have constructed a matrix model you might ask yourself ‘what would happen if I change one of the parameters in the model?’ For instance, how much does λ increase if I add 0.01 to matrix element a_{21} (the transition from the seed bank to small rosettes; $0.0039+0.01=0.0139$) in the Nodding Thistle model? Calculation of λ before and after the change shows that the projected population growth rate increases from 1.207 to 1.225. This change in λ not only depends on the magnitude of the change in the matrix element, but also on the sensitivity of λ to changes in that matrix element. This sensitivity ($\delta\lambda/\delta a_{ij}$) to small changes in a_{ij} can be calculated analytically using the left and right eigenvectors associated with λ . When comparing the λ -sensitivity values for all matrix elements one can find out in what element a certain increase has the biggest impact on λ .

However, a 0.01 increase in a survival matrix element is hard to compare to a 0.01 increase in a reproduction matrix element, because the latter is not bound between 0 and 1 and can sometimes take high values. Increasing matrix element a_{14} (number of seeds in the seed bank in the next year produced by an average large rosette) with 0.01 from 206.56 to 206.57 does not have a noticeable effect on λ . For comparison between matrix elements it can therefore be more insightful to look at the impact of proportional changes in elements: by what percentage does λ change if a matrix element is changed by a certain percentage? This proportional sensitivity is termed elasticity ($(\delta \log \lambda)/(\delta \log a_{ij}) = (a_{ij} \delta\lambda)/(\lambda \delta a_{ij})$). It turns out that the reproduction element a_{14} has a 16-fold higher λ -elasticity value as survival element a_{21} (0.0950 vs. 0.0059).

Since λ -elasticity values of all elements in a matrix sum to 1, they can also be considered as a measure of how much a matrix element contributes to λ , relative to the contributions of other elements. Quantifying the relative importance of different types of matrix elements to λ , elasticities, are therefore also very useful in comparative demography: different population and species can be compared with respect to how much e.g. survival or reproduction contributes to population growth. The reproduction transitions (i.e. dashed arrows in Fig. 1) of the Oystercatcher matrix model have a λ -elasticity total of 0.07, which is much lower than that of the Nodding Thistle model (elasticity total of the dashed arrows in Fig. 2 is 0.78). This places the Nodding Thistle near the fast end of a slow-fast continuum of species; and the Oystercatcher on the slow side. A cautionary note for comparison of elasticity patterns between species and

population is required though: elasticity values can also be correlated to matrix dimension and to λ itself. A matrix with a high λ will likely have higher elasticity values for reproduction elements than a matrix for the same species with a low λ .

Elasticity values can also be used to quantify the relative contributions of different life history loops within the life cycle of a species, the pathways that individuals take in the course of their lifetime. In the Oystercatcher example, for instance, three unique loops can be discerned: a four-year loop of new fledglings surviving for four years before producing new fledglings themselves, a similar five-year loop, and a ‘self-loop’ of surviving adults staying adults. Each of these loops has 1 or more transitions (arrows) unique for that loop. Since all transitions within a loop are equally important for the joint contribution of that loop to λ , each transition within a loop has the same elasticity value: all transitions in a loop have the same elasticity value as the unique transitions in the loop. The total loop elasticity is equal to the number of transitions in the loop times the elasticity values of a unique transition in that loop. In the Oystercatcher example the loop elasticities are 0.024, 0.313 and 0.663, respectively, which again adds up to 1. In other cases, such as that of the Nodding Thistle in Fig. 2, it is harder to discern all unique loops by hand. Luckily algorithms are now developed to do this automatically.

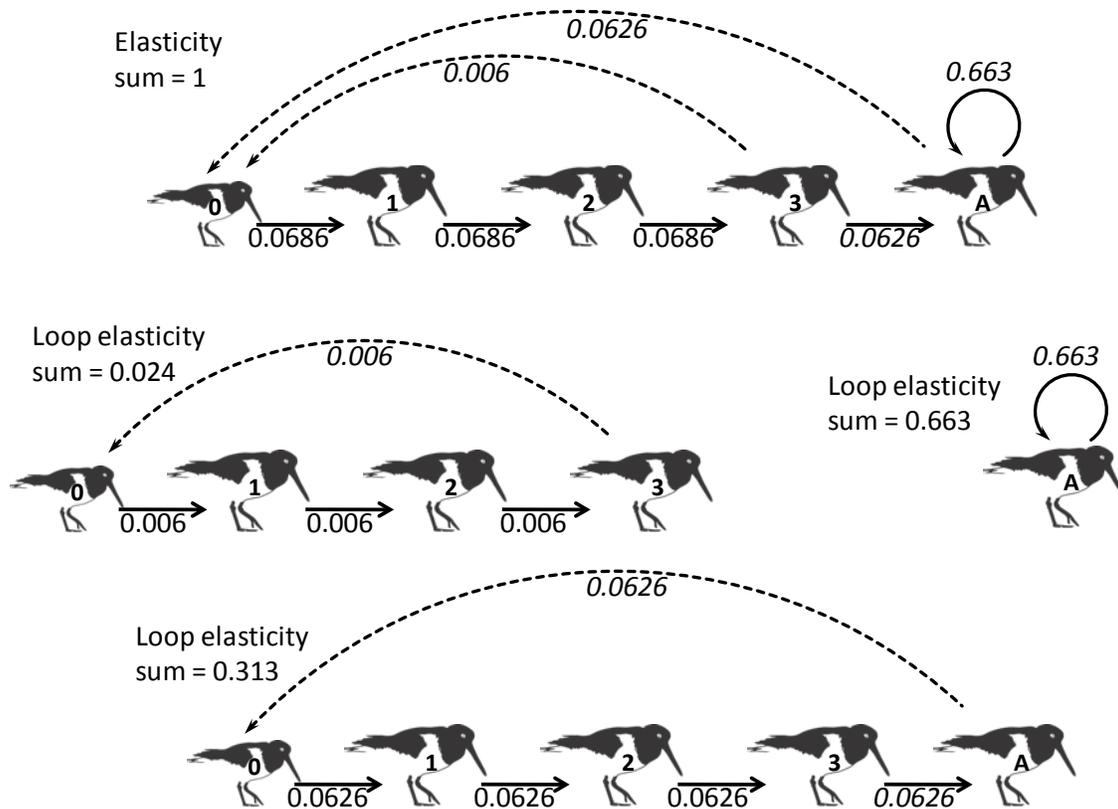


Figure 4. λ -elasticity values of transition in the Oystercatcher example. The life cycle graph contains 3 loops, each with at least one unique (italicized) transition. The unrounded elasticity values of all matrix elements always add up to 1. The shown elasticity values are rounded to add up to exactly 1 for clarity.

Sensitivity and elasticity values can also be calculated for lower-level parameters such as vital rates. Vital rate elasticities, however, most often add up to more than 1 because single matrix elements can be the products of multiple vital rates. It therefore depends on the vital rate construction of the matrix model what the sum of the vital rate elasticities is. This is not a problem for comparisons between populations or years of the same species studied with the same model. For comparisons between different types of models this is a problem. The best solution for cross-study comparisons seems to be to cast the different models of these studies into the same general vital rate structure, and then compare vital rate elasticities across studies.

So far we have focused on the (relative) sensitivity of λ to small changes in model parameters. However, similar sensitivities can be calculated for any other model output, such as the stable stage distribution or reproductive values. It is also good to realize that these sensitivity and elasticity values are characteristics of the matrix that is being studied. As soon as the transition matrix is changed considerably, the sensitivity values will also change. Although these 'local' sensitivities will give a fair indication of what will happen to e.g. λ when larger perturbations occur, it is better to study in detail the often non-linear response of λ to a model parameter along a large range of values of that parameter.

IV. Variance Decomposition

“Why is the projected population growth rate of one studied population higher than that of another?” is a common research question. Obviously some of the model parameter estimates were different, but how much does each of the parameter differences contribute to the difference in λ between the populations? To answer such questions variance decomposition techniques have been developed, generally referred to as “Life Table Response Experiments” or “LTRE”. The basic idea of LTREs is that the contribution of a parameter deviation is approximated by multiplying that deviation and the λ -sensitivity of that parameter. As discussed above this is a rough approximation since sensitivity values are 'local' characteristics that often change non-linearly with changes in any model parameter. Still the linear approximation works reasonably well: adding up the contributions of the deviations in all parameters often results in a value that is within a $\pm 1\%$ range around the actual difference in λ . For instance, when the Welsh Oystercatcher population is contrasted with a German population (Fig. 5), the decomposition into contributions by vital rate differences fits very well (-0.01%). Model fit may deteriorate when the life histories that are being compared in the matrix models are increasingly different. In such cases the non-linear approximation is no longer satisfactory, and researchers might want to use second derivatives or the exact relationships between λ and each model parameter.

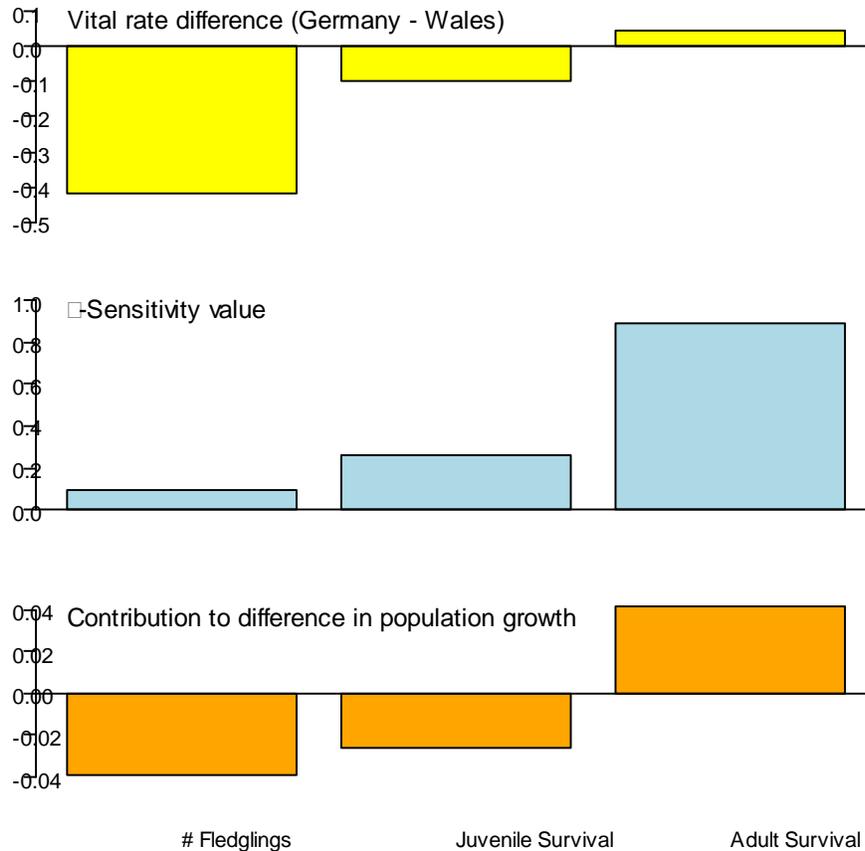


Figure 5. Steps of a decomposition (a fixed-effect Life Table Response Experiment) of the difference in λ between a German ($\lambda=0.950$) and a Welsh ($\lambda=0.974$) Oystercatcher population. The difference between the vital rates of the two populations are plotted in the top panel: especially the number of fledglings was lower in Germany, whereas adult survival was slightly higher compared to Wales. The second panel shows the λ -sensitivity values of the three vital rates (calculated with a reference matrix containing the mean vital rates across the two populations). The projected population growth rate (λ) is especially sensitive to changes in adult survival. Multiplying the vital rate difference (top panel) and the λ -sensitivity (middle panel) for each vital rate results in a linear approximation of the contributions to the difference in λ (bottom panel). The overall effect is negative (lower λ in Germany) due to smaller clutch size and lower juvenile survival, but is partly buffered by a positive effect of increased adult survival. The approximation fits well: the sum of the three contributions (-0.0239) is very close to the difference in λ (-0.0240).

This so-called ‘fixed-effect’ LTRE decomposes the deviation in λ for each separate matrix (representing e.g. a population or a treatment) compared to a chosen reference matrix. In some cases, however, you might not be as interested in how each separate site or year deviates in the contributions to λ , but rather in how vital rate variation contributed to the overall variance in λ . In such cases a ‘random-effect’ LTRE is more appropriate. In random-effect LTREs the variance of λ across years is decomposed into contributions of not only the variances of each vital rate but also into contributions of the covariances among vital rates.

V. Transient Dynamics

Matrix analyses based on the projected population growth rate (λ) or other asymptotic matrix properties assume that these are informative when studying the dynamics of a population and how it will respond to e.g. management or environmental change. However, as can be seen in Fig. 3, it takes some years before these asymptotic dynamics are reached. Furthermore, the realized population growth not only depends on λ but also on the stage distribution a population happens to be in. The Oystercatcher population simulated in Figure 3 is first decreasing, then increasing again, before steadily decreasing, while λ (0.974) was constant throughout.

The asymptotic properties can still inform researchers about how quickly asymptotic population behavior is expected to be reached. The ratio between the dominant eigenvalue and the second highest eigenvalue of a transition matrix is called the damping ratio. High damping ratios tell you that the dominant stable stage distribution is reached fairly soon.

Recently researchers have become increasingly interested in transient rather than asymptotic dynamics. The general notion is that transient dynamics (e.g. the first few years in Fig. 3) are more relevant for what happens in real populations that are never in stable state due to stochastic dynamics or disturbances. A wide arsenal of transient indices is now developed to study transient dynamics in response to all kinds of disturbances, and across a wide range of life histories.

VI. Stochastic Dynamics

As we have seen it takes some years with transient dynamics before asymptotic dynamics are reached. In the real world, however, environmental conditions (e.g. climate, competitors, predators) do not remain constant: every year is going to be different, resulting in different vital rates each year. As a consequence populations are pulled towards different ‘stable’ stage distributions each year. Population dynamics are therefore inherently stochastic in nature. Transition matrices can also be used to study stochastic dynamics.

Year-to-year variation in vital rates can be included in stochastic analyses in different ways. In simulations vital rate values can be drawn each simulated year from measured or assumed probability distributions of vital rate values. When using random draws for each vital rate extra care needs to be taken to make sure that the resulting transition matrix does not include biological impossibilities like survival rates larger than 100%. Some researchers therefore prefer another method of simulating population dynamics over long time spans: each year a single transition matrix is randomly chosen to multiply the current population vector with (Fig. 6). The advantage of this method is that all vital rate combinations are biologically realistic.

From stochastic simulations as in Figure 6 one can calculate the stochastic population growth rate, λ_s . To get a proper estimation of λ_s it is important to remove the initial transient dynamics caused by the arbitrarily chosen initial population structure. Elasticity analyses can also be done for λ_s . At the level of matrix elements stochastic elasticities again sum to 1. Stochastic elasticities, however, can be further split into an elasticity value of the mean of a matrix element and an elasticity value of the variance of that matrix element. Since a small increase in the variance of a matrix element can either increase or decrease stochastic population growth, λ_s -elasticity values of matrix element variances can be both positive and negative. Increases in matrix element means always have a positive effect on λ_s and these elasticity values are therefore always positive. Such stochastic elasticities can also be used to study whether there are relationships between the amount of variation in vital rates and how much vital rate variance

contributes to λ_s . Various of such stochastic variance decomposition techniques ('SLTRE') have recently been developed.

Population Viability Analyses often use stochastic simulations to estimate quasi-extinction risks. By repeating the stochastic simulation of Fig. 6 many times we can calculate how many years it takes for this hypothetical population of 1500 Oystercatchers to become smaller than 50 birds: 70 years (± 3.2 standard deviation). This is of course not a prediction but a projection of what would happen if the two transition matrices used in the simulation each have a 50% chance of occurrence each year. Ideally large numbers of annual matrices from the same population are used. If correlations with climatic drivers can be made, stochastic simulation can then be used to study how the quasi-extinction risk changes with altered occurrence of e.g. good or bad years. Please read more about such analyses in the chapter on Population Viability Analysis.

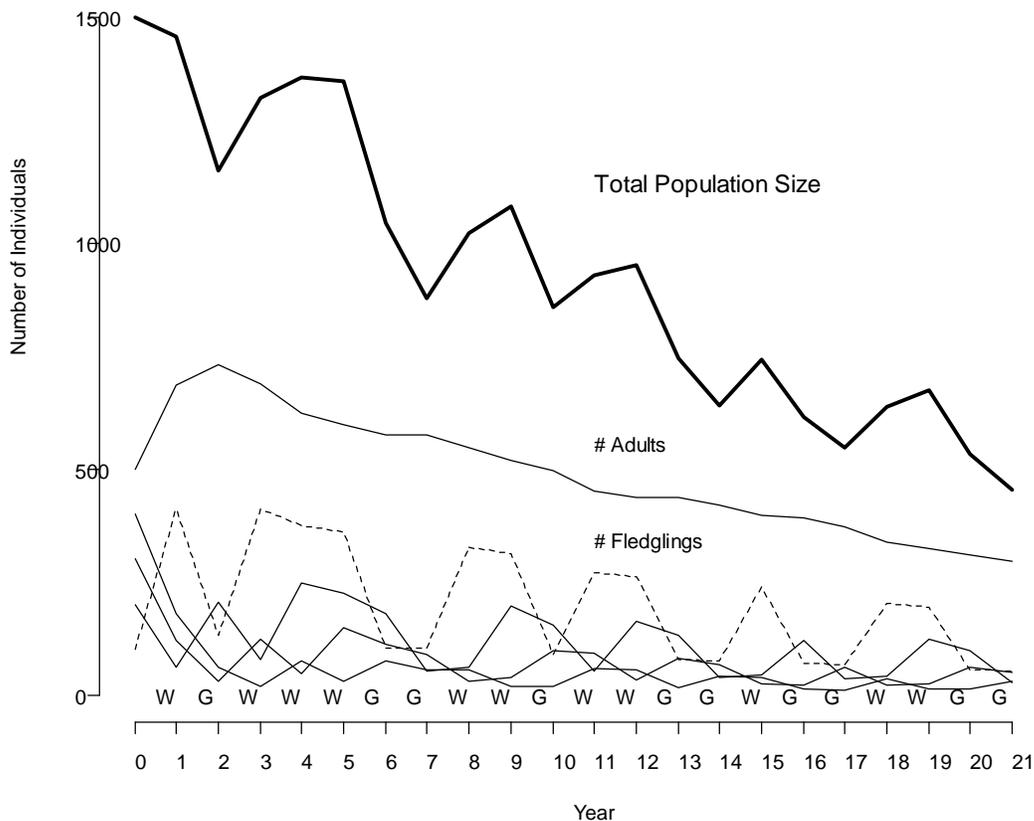


Figure 6. A stochastic simulation of an Oystercatcher population. The initial population of 1500 is the same as in Fig. 3. At each simulated year the population vector (with the number of individuals in each of the 5 stage classes) is multiplied with a randomly chosen transition matrix: each of two matrices had a 50% chance to be drawn each year. Ideally a pool of matrices representing observed data from a number of different years in the same population is used for such stochastic simulations. For illustrative purposes only, we here use matrices from two different matrices: W = Wales and G = Germany (see also Fig. 5). The letters in the graph indicate which transition matrix was randomly drawn and applied each year in this simulation. Although both matrices W and G project asymptotic population declines, the simulated population is actually growing in some years due to changes in the distribution of individuals over the age classes

VII. Integral Projection Models

One problem with size-based stage classifications is that it can be hard to find clear borders between one size group and the next: the sizes of individuals in a population often follow a continuous distribution, and vital rates mostly show gradual change with size (e.g. Fig. 7). Furthermore, the choice of the number of size classes is not without consequences: matrix dimension can have profound impact on e.g. the projected population growth rate (λ). This is especially the case in long-lived, slow-growing species like trees: if there are only a few size classes, progression to the next class will be rare. However, according to such model, it would still be possible for some individuals to reach the size of large reproductive tree in only a few years. Such biologically unrealistic ‘short-cuts’ in the life history increase λ disproportionately. However, when the variation in growth is relatively large compared to the range of observed sizes of individuals (as can be seen in Fig. 7), lower numbers (e.g. ≥ 7) of size classes will suffice.

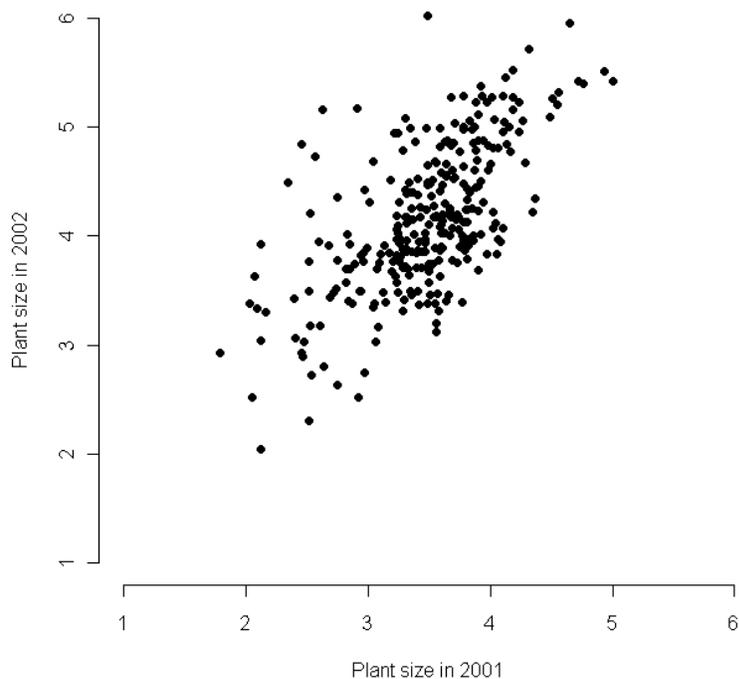


Figure 7. Relationship between plant size and the size of the same plants 1 year later in a Devil’s Bit Scabious (*Succisa pratensis*) population (E. Jongejans and H. de Kroon 2005 J. Ecol. 93:681-692). No distinct size classes are apparent and there is large variation in the size of individuals that were the same size the year before. In this case plant size is the natural log of the product of the number of leaves and maximum leaf length.

Researchers have tried to deal with the problem of seemingly arbitrary size classification by using an algorithm developed by Moloney. This algorithm aims to optimize the number of distinctive classes taking the sample and distribution errors into account. Another method is to use statistical tests to find size classes with significantly different vital rates. However, these

methods are strongly driven by sample size rather than based solely on the species' life history. An elegant solution has been introduced by Ellner and co-workers in 2000: no size classification at all. In their Integral Projection Models (IPMs) vital rates are continuous functions of size; functions that can be copied directly from statistical regression analyses. An additional advantage is that often fewer parameters need to be fitted compared to matrix models with different vital rates for each size class. Though IPMs contain continuous functions, it is still necessary to turn them into sufficiently large matrices before matrix algebra can be applied. In this way IPMs combine the best of two worlds: parameterization and interpretation along continuous state variables, and the analytical toolbox of discrete matrix models.

IPMs are becoming increasingly popular in studies with continuous state variables (e.g. size), and all kind of combinations of discrete classes (e.g. seed banks) and continuous state variables are possible. An interesting development is to make vital rates not only functions of size but also of time within years. In some cases, for instance, winter and summer survival are modeled as separate vital rates, and if sufficient data are available survival rates could be continuous functions of size and time between annual census days. Future studies will have to show what the added value is of adding such detail to projection models.

For comparative demography IPMs may also prove to be very useful because they solve the problem that different matrix studies use a range of matrix dimensions. Still, also in comparative studies based on IPMs, decisions will have to be made about how to compare the various vital rate functions and definitions between studies.

IPMs are also useful for studying the population-level impact of environmental factors like soil conditions, climate, management and biotic interactions. These explanatory factors can be included in the statistical regression analyses of the vital rates. In such Hierarchical Population Models the projected population growth rate becomes a function of environmental drivers. For instance, one can then answer research questions like “how much is population size affected by cold winters, and how much of that response is due to changes in survival, growth or reproduction?” Population size itself can also be included as a driver of vital rates. The asymptotic behavior of such density-dependent models is somewhat different from that of matrix models in which density-dependence is not included explicitly. Luckily, analytical tools for density-dependent matrix models have recently been developed.

See Also the Following Articles

Age structure, Conservation biology, Demography, Environmental stochasticity, Population ecology, Population viability analysis, Spatial spread, Stage structure,

Glossary

elasticity the proportional change in model output (e.g. the projected population growth rate, λ) when a model parameter (e.g. matrix element a_{ij}) is perturbed by a small percentage: $\delta \log(\lambda) / \delta \log(a_{ij})$

integral projection models (IPM) a discrete-time structured population model in which one or more continuous state variables (e.g. individual size). The advantage of integral projection models over matrix models is that no class borders have to be imposed when these are not apparent from the data, that often fewer parameters need to be estimated, and that individual variation can generally be included and studied in more detail. In order to apply the matrix algebra toolbox, the continuous integral projection models need to be translated into transition matrices with many, near-continuous classes.

life cycle graph a schematic representation of the local demographic processes in a population. The population is structured in age and/or size classes, which are connected by arrows that represent how an average individual in a class contributes to the number of individuals in the recipient class one time step later. Contributions can be either through survival and growth or through reproduction.

loop analysis life cycle graphs of population often consist of multiple loops. With loop analysis (based on loop elasticities) the relative importance of each of these loops for e.g. population growth can be studied.

projected population growth rate the dominant eigenvalue (λ) is an analytical property of a transition matrix. It gives the asymptotic growth rate of the population if the demographic rates in the matrix remain constant over many time steps.

sensitivity the change in model output (e.g. the projected population growth rate, λ) when a model parameter (e.g. matrix element a_{ij}) is perturbed a little bit: $\delta\lambda/\delta a_{ij}$

stable stage distribution the proportional distribution of individuals over the stage classes becomes stable if the same transition matrix is applied to a population vector for many consecutive time steps.

transient dynamics until the stage distribution becomes stable, changes in population size and structure are determined not only by the transition matrix but also by the current population structure. These transient dynamics last until asymptotic dynamics are reached.

vital rate demographic processes that are the building blocks of population models. E.g. survival, growth (i.e. any size or age change of surviving individuals), number of flowers, recruitment probability, etc. A vital rate can occur in multiple matrix elements. Matrix elements consist of one or more vital rates.

Further Reading

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