OIKOS 96: 56–61, 2002

Stage-classified matrix models and age estimates

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Barot, S., Gignoux, J. and Legendre, S. 2002. Stage-classified matrix models and age estimates. – Oikos 96: 56–61.

When the size of individuals is a better indicator of their chances to survive, grow, and reproduce than their age, the suitable matrix population model is stage-classified. Cochran and Ellner developed a method to assess age-based parameters from such models. We present here, for these age estimates, simplified formulas that are valid whenever there is neither retrogression nor fission: individuals may only die, survive in the same stage, or survive and recruit to the next stage. Our formulas enable one to understand better why, and under which hypotheses, it is possible to compute age estimates from a stage-classified model, and point out some limitations of the method. These limitations in fact come from the basic hypothesis of stage-classified matrix models: stage is considered to be the only variable that influences survival and recruitment rates. As a consequence, age estimates using stage-classified models should be valid if the stages describe precisely enough the life cycles of the studied species, and particularly if senescence is taken into account.

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For animals such as birds or mammals, survival and fecundity are usually said to depend mostly on age, whereas size is more relevant in the study of plant dynamics (Caswell 2001: Chapter 3). Indeed, plants are modular organisms, and are generally much more plastic in their growth than animals (Watkinson and White 1985, Begon et al. 1990). Consequently, the relation between age and size (or stage) is obscure in plants. For example, some saplings may remain alive during many years without growing, because of a poor access to light. But when a neighbour adult tree dies, more light reaches the saplings, and they may start to grow again (Kobe et al. 1995, Batista et al. 1998). In this way, plasticity is often critical for plants: they do not move but plasticity enables them to react to environmental variations.

Because of this plant propensity for plasticity, plant matrix models are usually stage- or size-classified (Caswell 2001: Chapter 4), as opposed to age-classified models. More generally, whenever the size or the stage of individuals is a better indicator of their chances to survive, grow, and reproduce, the suitable matrix population model is stage-classified. In this case, for the so-called Lefkovitch matrices, recruitment probabilities (g_i, survival and recruitment) appear on the sub-diagonal, and survival probabilities (p_i, survival in the same stage) on the diagonal. In the second case, for the so-called Leslie matrices, survival probabilities appear on the sub-diagonal, and there are no real recruitment probabilities. This difference between the two kinds of matrix models enables one to model plasticity and to account for the variability in the age at which individuals enter each successive stage.

Although age is not explicit in a Lefkovitch matrix, the way such a model is built enables one to assess ages in a stage-classified population (Cochran and Ellner 1992), simply because a transition matrix is computed for a given time interval (often a year). Caswell re-described the method in the general context of Markov chains (Caswell 2001: Chapter 5). We present here some simplified formulas for these age estimates (displayed synthetically in Table 1) that are valid in a sub class of

Accepted 19 June 2001

ISSN 0030-1299

Table 1. Simplifications of the formulas for the mean and the variance of some age-based parameters (Cochran and Ellner 1992) in the general case of a population classified into n stages, with only survival probabilities (p), and recruitment probabilities (g), no fission and no retrogression. λ is the asymptotic growth rate of the population (largest eigenvalue of the transition matrix). For simplification and by convention the value 1 was attributed to g_n which is not biologically defined.

Variable description	Variable name	Mean	Variance
Time spent in stage s by individuals that have reached stage s	X_s	$\mathrm{E}(X_s) = \frac{1}{1-p_s}$	$\mathrm{Var}(X_s) = \frac{p_s}{(1-p_s)^2}$
"Age of residence" in stage s	ψ_s	$S_s = \mathrm{E}(\psi_s) = \sum_{i=1}^{s} \frac{1}{1-p_i}$	$\mathrm{Var}(\psi_s) = \sum_{i=1}^{s} \frac{p_i}{(1-p_i)^2}$
Age when first reaching the stage s from the first stage	$\tau_{\mathrm{seed},s}$	$\mathrm{E}(\tau_{\mathrm{seed},s}) = 1 + \sum_{i=1}^{s-1} \frac{1}{1-p_i}$	$\mathrm{Var}(\tau_{\mathrm{seed},s}) = \sum_{i=1}^{s-1} \frac{p_i}{(1-p_i)^2}$
Remaining life span for an individual in stage s	Ω_s	$\mathrm{E}(\Omega_s) = \sum_{i=s}^{n} \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_i} \right)$	$\mathrm{Var}(\Omega_s) = \sum_{i=s}^{n} \left[\frac{1+p_i}{(1-p_i)g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} - \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right)^2 \right]$
Total conditional life span of individuals having reached stage s	Λ_s	$\mathrm{E}(\Lambda_s) = \sum_{i=s+1}^{n} \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right) + \sum_{i=1}^{s} \frac{1}{1-p_i} + 1$	$\mathrm{Var}(\Lambda_s) = \sum_{i=s}^{n} \left[\frac{1+p_i}{(1-p_i)g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} - \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right)^2 \right] + \sum_{i=1}^{i} \frac{p_i}{(1-p_i)^2}$
Age of individuals in stage s under the assumption of stable stage distribution	Y_s	$y_s = \mathrm{E}(Y_s) = \sum_{i=1}^{s} \frac{1}{1-p_i\lambda^{-1}}$	$\mathrm{Var}(Y_s) = \sum_{i=1}^{s} \frac{p_i\lambda^{-1}}{(1-p_i\lambda^{-1})^2}$

models, when there is neither retrogression nor fission, and when there is a unique type of newborn (individuals may only die, survive in the same stage, or recruit to the next stage). These formulas are useful because: (1) Linking directly age estimations to matrix parameters, they enable one to compute the age estimates without any particular software; (2) they enable one to derive the sensitivity of these age estimates to the matrix parameters; (3) the way these simple formulas were derived points out the hypotheses on which the method relies.

Results

For each stage, it is possible to compute the mean (E) and the variance (Var) of various age-based life-history parameters (Cochran and Ellner 1992), using Cochran and Ellner's notation: the age in the ith stage (Y_i), the "age of residence" in the ith stage (ψ_i), the "conditional remaining life span" of individuals in the ith stage (Ω_i), the time to reach the ith stage from the seed (first) stage ($\tau_{\mathrm{seed},i}$), the total conditional life span of individuals that have reached the ith stage (Λ_i) (Λ_i is the sum of $\tau_{\mathrm{seed},i}$ and Ω_i). The "age of residence" (which is the original term used by Cochran and Ellner) denotes the age of individuals found in a given stage and not the amount of time spent in this stage. Similarly, the expression "conditional remaining life span" will be kept throughout the paper, but it denotes more precisely the remaining life span of individuals, given that they are in stage s at a given time.

Y_i is defined in such a way that $\mathrm{E}(Y_i)$ and $\mathrm{Var}(Y_i)$ are computed under the assumption that a stable stage distribution has been reached and depend on the asymptotic growth rate (and thus depend on fecundities) (Cochran and Ellner 1992). On the contrary, $\psi_i(t)$ is defined as the expected frequency distribution of ages (t) of the individuals of a cohort of newborns while they are in stage i. Consequently, $\mathrm{E}(\psi_i)$ and $\mathrm{Var}(\psi_i)$ neither depend on the asymptotic growth rate nor on fecundities (Cochran and Ellner 1992). Thus, the means and the variances of Y_i and ψ_i are two different ways to measure the relationship between age and stages.

Estimation of mean ages

P(Ev1) and P(Ev1 | Ev2) are defined, respectively, as the probability of event "Ev1" and the probability of event "Ev1" conditional on the occurrence of event "Ev2". X_s is the time spent in stage s by individuals that have reached this stage, and p_s and g_s are, respectively, the survival and recruitment rates in stage s. n is the number of stages in the model. We have:

$$\mathrm{P}(X_s = i) = p_s^{i-1}(1 - p_s)$$

and

$$\mathrm{E}(X_s) = \sum_{i=1}^{+\infty} i p_s^{i-1}(1 - p_s),$$

the index i running over the years spent in stage s.

Consequently, since

$$\sum_{i=1}^{+\infty} i x^{i-1} = (1-x)^{-2}$$

(classical geometric series result, for $x \in]-1, 1[$):

$$\mathrm{E}(X_s) = \frac{1}{1-p_s}. \quad (1)$$

With $r_{i,s}$ defined as the event "stage i has been reached by an individual originally in stage s" ($i \geq s$), $r_{s+1,s}$ is the probability for stage s individuals being recruited to the next stage before dying. We have then:

$$\mathrm{P}(r_{s+1,s}) = \sum_{i=1}^{+\infty} P \text{ (being recruited before dying after } i \text{ years spent in stage } s),$$

and

$$\mathrm{P}(r_{s+1,s}) = \sum_{i=1}^{+\infty} p_s^{i-1} g_s.$$

Consequently, since $\Sigma_{i=1}^{+\infty} x^{i-1} = (1-x)^{-1}$ (classical geometric series result, for $x \in]-1, 1[$):

$$\mathrm{P}(r_{s+1,s}) = \frac{g_s}{1-p_s}. \quad (2)$$

As the expected value of a sum is the sum of the expected values, and since we have

$$\psi_s = \sum_{i=1}^{s} X_i,$$

we can derive from eq. 1 the expression for the mean age of residence in stage s:

$$S_s = \mathrm{E}(\psi_s) = \sum_{i=1}^{s} \frac{1}{1-p_i}. \quad (3)$$

Consequently, individuals first reach the stage s on average at age $S_{s-1} + 1$, giving

$$\mathrm{E}(\tau_{\mathrm{seed},s}) = 1 + \sum_{i=1}^{s-1} \frac{1}{1-p_i}. \quad (4)$$

The mean remaining life span of individuals in stage s, is the sum of the conditional expectations of time spent in each stage, under the condition that these stages have been reached before death:

$$\mathrm{E}(\Omega_s) = \sum_{i=s}^{n} \mathrm{E}(\text{time spent in stage } i \mid r_{i,s}) \mathrm{P}(r_{i,s}).$$

Then, using eq. 1, and since E(time spent in stage $i \mid r_{i,s}) = \mathrm{E}(X_s)$:

$$\mathrm{E}(\Omega_s) = \sum_{i=s}^{n} \frac{1}{1-p_i} \mathrm{P}(r_{i,s}).$$

We have then, due to eq. 2, and since we have if $i > s$

$$\mathrm{P}(r_{i,s}) = \prod_{j=s}^{i-1} \mathrm{P}(r_{j+1,j}):$$

$$\mathrm{E}(\Omega_s) = \frac{1}{1-p_s} + \sum_{i=s+1}^{n} \left(\frac{1}{1-p_i} \prod_{j=s}^{i-1} \frac{g_j}{1-p_j} \right). \quad (5)$$

After rearrangement and attributing by convention and to simplify the expression, the value 1 to g_n which is not biologically defined:

$$\mathrm{E}(\Omega_s) = \sum_{i=s}^{n} \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right). \quad (6)$$

Since, by definition, the total conditional life span of individuals that have reached stage s is the sum of the mean remaining life span (eq. 6) and the mean age to reach the considered stage (eq. 4) ($\Lambda_s = \Omega_s + \tau_{\mathrm{seed},s}$),

$$\mathrm{E}(\Lambda_s) = \sum_{i=s+1}^{n} \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right) + \sum_{i=1}^{s} \frac{1}{1-p_i} + 1.$$

The average age of individuals in stage s, y_s, was derived by analogy with the matrix formulas for the mean age of residence and the mean age (Cochran and Ellner 1992) and the above simplified formula for the mean age of residence (eq. 3):

$$y_s = \mathrm{E}(Y_s) = \sum_{i=1}^{s} \frac{1}{1-p_i \lambda^{-1}}.$$

Estimation of age variances

Simplified formulas can also be computed for variances. First,

$$\mathrm{E}(X_s^2) = \sum_{i=1}^{+\infty} i^2 p_s^{i-1} (1-p_s).$$

Since

$$\sum_{i=1}^{+\infty} i^2 x^{i-1} = (1+x)(1-x)^{-3}$$

(classical geometric series result, for $x \in]-1, 1[$), this leads to:

$$\mathrm{E}(x_s^2) = \frac{1+p_s}{(1-p_s)^2} \quad (7)$$

and

$$\mathrm{Var}(X_s) = \mathrm{E}(X_s^2) - \mathrm{E}(X_s)^2 = \frac{p_s}{(1-p_s)^2}. \quad (8)$$

As the time spent in each stage is independent of the time spent in the other stages (implicit hypothesis of the model), the X_i variables are independent. Then, since $\psi_s = \Sigma_{i=1}^{s} X_i$, and due to eq. 8:

$$\mathrm{Var}(\psi_s) = \sum_{i=1}^{s} \frac{p_i}{(1-p_i)^2}. \quad (9)$$

To compute the variance of the remaining life span, the same method as for its mean can be used, supposing again that the times spent in the different stages are independent:

$$\mathrm{Var}(\Omega_s) = \sum_{i=s}^{n} \mathrm{Var}(\text{time spent in stage } i), \quad \text{and}$$

$$\mathrm{Var}(\Omega_s) = \sum_{i=s}^{n} (\mathrm{E}((\text{time spent in stage } i)^2) - \mathrm{E}^2(\text{time spent in stage } i)).$$

Then we have, using conditional probabilities:

$$\mathrm{Var}(\Omega_s) = \sum_{i=s}^{n} [\mathrm{E}(X_i^2|r_{i,s})\mathrm{P}(r_{i,s}) - \mathrm{E}^2(X_i|r_{i,s})\mathrm{P}^2(r_{i,s})].$$

As for eq. 6, using eqs 1, 5, 7, and after rearrangement:

$$\mathrm{Var}(\Omega_s) = \sum_{i=s}^{n} \left[\frac{1+p_i}{(1-p_i)g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} - \left(\frac{1}{g_i} \prod_{j=s}^{i} \frac{g_j}{1-p_j} \right)^2 \right]. \quad (10)$$

Supposing again that the times spent in different stages are independent, $\mathrm{Var}(\Lambda_s) = \mathrm{Var}(\Omega_s) + \mathrm{Var}(\psi_s)$ where $\mathrm{Var}(\Omega_s)$ and $\mathrm{Var}(\psi_s)$ have already been computed (eqs 10 and 9).

By analogy with the matrix formulas for the variance of the age of residence and the variance of the age (Cochran and Ellner 1992) and the above simplified formula for the variance of the age of residence (eq. 9):

$$\mathrm{Var}(Y_s) = \sum_{i=1}^{s} \frac{p_i \lambda^{-1}}{(1-p_i\lambda^{-1})^2}.$$

Sensitivity of age estimations to the matrix parameters

It is then straightforward to derive from the above equations the sensitivities of the considered age-based parameters to the matrix parameters. For example, for $s2 < s1 - 1$:

$$\frac{\partial S_{s1}}{\partial p_{s2}} = \frac{\partial \mathrm{E}(\tau_{\mathrm{seed},s1})}{\partial p_{s2}} = \frac{1}{(1-p_{s2})^2}, \quad (11)$$

$$\frac{\partial S_{s1}}{\partial g_{s2}} = \frac{\partial \mathrm{E}(\tau_{\mathrm{seed},s1})}{\partial g_{s2}} = 0,$$

$$\frac{\partial \mathrm{Var}(\psi_{s1})}{\partial p_{s2}} = \frac{\partial \mathrm{Var}(\tau_{\mathrm{seed},s1})}{\partial p_{s2}} = \frac{1+p_{s2}}{(1-p_{s2})^3} \quad \text{and} \quad (12)$$

$$\frac{\partial \mathrm{Var}(\psi_{s1})}{\partial g_{s2}} = \frac{\partial \mathrm{Var}(\tau_{\mathrm{seed},s1})}{\partial g_{s2}} = 0.$$

Discussion

The simplified formulas presented here are less general than the original ones computed by Cochran and Ellner (1992): they are only valid for transition matrix without retrogression (individuals may not grow into a less developed stage or become smaller) or fission (vegetative reproduction). Yet, they emphasise the direct link between some age-based parameters and the matrix parameters, i.e. the probabilities to survive in the same stage, and to be recruited to a more developed stage. They also enable one to understand in an intuitive way why age is implicitly taken into account in stage-classified matrix model and under which hypotheses.

Thanks to the simplified formulas it is in particular possible to derive explicitly the sensitivity of the age-based parameters to the vital rates or to compare the standard deviation and the mean of age-based parameters. It is, for example, easy to prove, using eqs 1 and 8, that the mean time spent in stage i by individuals that have reached this stage, $\mathrm{E}(X_i)$, is always higher than its standard deviation, $\sigma(X_i)$, but that the ratio of this mean and this standard deviation goes to zero when the survival rate in the stage (p_i) goes to 1 (which is likely to be the case for long-lived organisms). Consequently, summing the inequalities $\mathrm{E}(X_i) > \sigma(X_i)$ and because the square of a sum of positive terms is higher than the sum of the squares of the terms, it is clear that, whenever there is no retrogression and no fission in a life cycle, the mean age of residence in a stage is always higher than its standard deviation, whatever the survival and recruitment rates. Moreover, it is meaningful that: (1) The sensitivities to survival rates of mean and variance of age of residence both increase with the considered survival rates (the derivatives of the expressions 11 and 12 with respect to p_{s2} are always positive). (2) The sensitivity of the variance is higher than the sensitivity of the mean, whatever the survival rate. Age estimates are much more sensitive to survival rates when these rates are high. Consequently, when survival rates are high, vital rates must be measured very precisely, i.e.

using a large sample of individuals in the considered stages, if precise age-based parameters estimations are to be derived. Such a problem is likely to arise for long-lived organisms if too few stages are used.

Besides, it was found that the mean and variance of the "age of residence" do not depend on recruitment rates, which has not been noticed before. This results from the fact that the time spent in a stage only depends on the probability of staying in the stage (p = survival in the same stage) as opposed to the probability of leaving the stage ($1-p$ = death + survival and recruitment to the next stage). In the case of a matrix model including some retrogression, such a result would not hold: the mean and the variance of the "age of residence" would depend on recruitments rates that determine the probability of coming back to the same stage.

The computation of the formulas for the variances of age-based parameters also emphasises an implicit hypothesis of the age estimation method: the times spent in the successive stages are statistically independent. Concretely, it means that in order to derive the variances, we must assume that what happens in the first stages of an individual (time spent in each stage, growth speed) does not influence the time spent in the later stages. This hypothesis seems to be biologically questionable since: (1) Environmental variations are frequently auto-correlated in space, which leads to the existence of individuals that grow quickly with high survival rates in favourable patches during all their life; (2) Plasticity in growth is not infinite. If for some reason an individual remains for many years in the same stage (low growth rate) it might have a cost that will result in lower survival rate, and recruitment rate in the next stages. Point (1) would lead to an underestimation of age variances by Cochran and Ellner's (Cochran and Ellner 1992) method, while point (2) could lead to an overestimation.

More generally, to asses the time spent in each stage, Cochran and Ellner's method relies on another hypothesis: survival and recruitment rates in a stage do not depend on the time already spent in the considered stage. When we computed $E(X_s)$, the mean number of years spent in a stage with a survival rate p_s, we could have directly stated that X_s follows a geometric discrete distribution, which relies on the hypothesis that the probability of the awaited event (here the death of an individual or its recruitment to the next stage) does not change in time. Individuals are supposed to be able to stay indefinitely in each stage. This hypothesis is again questionable: (1) It is likely that the true survival rate of individuals in the last stage (and even possibly in the intermediate stages), i.e. the oldest individuals (or the oldest individuals in a stage), will decrease with the number of years spent in the stage. This is a consequence of senescence, which is a wide-spread phenomenon in plants (Watkinson 1992). (2) The true recruitment rates probably also depend on the number of years already spent in the considered stages. For example, if a stage is defined as a size-class, the longer some individuals stay in this stage, the taller they grow, and the more likely they are to recruit to the next stage (p decreases while g increases). This case and point (1) should lead to an overestimation of mean ages.

The biases pointed out in the last two paragraphs seem to limit the utilisation of stage-classified matrix models in order to estimate age-based parameters. However, it must be noted that the hypotheses on which those estimates rely are not ad hoc hypotheses proposed to compute easily and analytically the age-based parameters, either using the whole matrices (Cochran and Ellner 1992, Caswell 2001: Chapter 5) or, as in the present paper, using basic probability formulas. Although they are too often forgotten, these hypotheses are basic to any stage-classified matrix model, and can be summarised in one sentence: the stage of an individual is the only variable influencing its survival and recruitment rates (Caswell 2001: Chapters 3, 4). The age and the time already spent in a stage are supposed not to influence survival and recruitment rates. Similarly, it is always supposed that the time spent in the different stages are independent variables; otherwise it would mean that, in a given stage, there exist individuals with different vital rates: if some individuals have higher survival rates than the others as juveniles, and if the reverse holds when these individuals become adults, adult and juvenile period durations will be negatively correlated.

As mentioned by Cochran and Ellner the non-validity of these hypotheses leads to biases in the age estimates (Cochran and Ellner 1992). The validity of the results of a model always depends on the verification of the model assumptions. It is particularly the case for Cochran and Ellner's formula, but it is also the case for traditional matrix model analysis. For example, Ehrlén (2000) included historical effects in a matrix model, i.e. the vital rates of individuals did not depend only on their current stage but also on the stages they occupied formerly. Such historical effects seem to be frequent and it was found that they lead to biases in the asymptotic growth rates and stable stage distributions.

Enright et al. (1995) found that age-based parameters estimated using stage-classified matrix models depend on the numbers of stages used. This seems again to be a strong limitation to the age estimation method. However, the problem is likely to be mostly due to variations in the strength of the violation of the basic matrix model hypothesis mentioned above. For example, according to the number of stages, the model will describe partially, or not at all, the senescence of the oldest individuals (decrease in survival rates). If senescence is taken into account by the stage-classified model – for example if there is a stage for the tallest and probably oldest individuals – the fact that vital rates depend also

on age might only lead to a slight bias in age estimates. In a general way, a stage-classified model must describe a life cycle precisely for the derived age estimates to be valid.

This issue arises from the fate of individuals, especially plant individuals, depending generally both on their size and their age (Werner and Caswell 1977, Lacey 1986, Stoll et al. 1994). Such a process could be taken into account by matrix models that use classes of individuals defined both by their age and their size (Law 1983, Law and Edley 1990), or by individual-based simulation models (Huston et al. 1988, Judson 1994). Such models could provide better estimates of age-based parameters than Cochran and Ellner's method (Cochran and Ellner 1992), but need huge data sets to be parameterised thoroughly. A fruitful way to test Cochran and Ellner's estimation method and the matrix-model hypotheses on which they rely would consist in building matrix models for plant populations whose real age distributions are known, for example by annual growth ring countings.

Acknowledgements – The work was supported by funding from the CNRS-ORSTOM SALT program (GCTE core research project).

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