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Building matrix population models when individuals are non-identifiable

Carlos Hernandez-Suarez [a,c,*], Paula Medone [b], Carlos Castillo-Chavez [c,d], Jorge Rabinovich [b]

[a] Facultad de Ciencias, Universidad de Colima, Bernal Díaz del Castillo 340, Colima 28040, Mexico
[b] Centro de Estudios Parasitológicos y de Vectores (CEPAVE, CCT La Plata, CONICET- UNLP) La Plata, Prov. de Buenos Aires, Argentina
[c] Simon A. Levin Mathematical and Computational Modeling Sciences Center, Arizona State University, Tempe, AZ 85287-3901, U.S
[d] Departamento de Ingeniería Biomédica, Universidad de los Andes, Bogotá 111711 Colombia

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ABSTRACT

Matrix Population Models (MPM) are among the most widely used tools in ecology and evolution. These models consider the life cycle of an individual as composed by states to construct a matrix containing the likelihood of transitions between these states as well as sexual and/or asexual per-capita offspring contributions. When individuals are identifiable one can parametrize an MPM based on survival and fertility data and average development times for every state, but some of this information is absent or incomplete for non-cohort data, or for cohort data when individuals are not identifiable. Here we introduce a simple procedure for the parameterization of an MPM that can be used with cohort data when individuals are non-identifiable; among other aspects our procedure is a novelty in that it does not require information on stage development (or stage residence) times, which current procedures require to be estimated externally, and it is a frequent source of error. We exemplify the procedure with a laboratory cohort dataset from *Eratyrus mucronatus* (Reduviidae, Triatominae). We also show that even if individuals are identifiable and the duration of each stage is externally estimated with no error, our procedure is simpler to use and yields the same MPM parameter estimates.

1. Introduction

The life history traits of a species (e.g., size at birth, growth rate, age and size at maturity, age-specific reproductive investment, number and size of offspring, age-specific survival, and lifespan) are frequently estimated by laboratory or field studies and used to estimate survival, development times, and fertility of a cohort or a population. From these studies the construction of age-specific life tables and maternity tables provide the data necessary for the best estimates of the basic demographic parameters: r (intrinsic rate of natural increase), R_0 (net reproductive rate), and $\bar{T}$ (average generation time). However, in many species it frequently happens that age cannot be identified (or it is extremely costly to do so) and the survival, development times, and fertility are based on some class category (state, size, or any other practical category to classify individuals as they age). In these situations, life history trait (LHT) analysis and population projections have resorted to the use of matrix models.

Since Caswell (2001) published his now classic book on Matrix Population Models these models are among the most widely used tools in theoretical and applied ecology and evolution (ecological and evolutionary population analysis, population viability, living resources management). Among the most influential works on the subject are the pioneering papers by Leslie (1945, 1948a, b) followed by those of Lefkovitch (1965) and Usher (1966). More recently, Ebert (1999) and Caswell (2001, 2006) among others, developed practical methods for applied biologists and ecologists, that have been applied in a broad range of marine and terrestrial species.

Our work is embedded in the theory of life histories, providing an improvement over the existing procedures to carry out a formal analysis of the evolution of an organism's life cycle. Plants and animals show different demographic strategies, and life history theory seeks an interpretation of their variation from a natural selection point of view. A life history strategy has been defined as the"age- and stage-specific pattern" (Flatt and Heyland, 2011), including the timing of events that make up an organism's life cycle. Contrary to the study of life cycles, that has been predominantly descrip-

* Corresponding author.
E-mail addresses: carlosmh@mac.com (C. Hernandez-Suarez), paulamedone@gmail.com (P. Medone), ccchavez@asu.edu (C. Castillo-Chavez), jorge.rabinovich@gmail.com (J. Rabinovich).

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tive, since the seminal work of Stearns (1992) and Roff (1992) the theory of life histories has been highly mathematical, resorting to the principle of optimality because of the constraints to, and trade-offs between life-history traits; this approach was fruitful in leading towards general principles able to provide a predictive framework, and has been partially achieved invoking natural selection, a framework that allowed frequent experimental laboratory tests of the processes that lead to optimal phenotypes; among those processes the physiological and genetic ones are increasingly becoming key factors in our interpretation of the evolution of life histories. Predictions of these recent approaches to life history theory depend critically upon an adequate parameter estimate of the basic life cycle events (growth, survival and the schedule of reproduction); however, this was not enough, for the natural selection process behind the life history theory requires a population approach, and those life cycle parameters (e.g., timing of survival and reproduction schedules) needed to be converted into probabilities of demographic events; this requirement was fulfilled by the first Matrix Population Model (MPM) derived from life cycle parameters (Lefkovitch, 1965), an approach that flourished quickly with the rich developments carried out by Caswell (2001) and Manly (1990). Those developments included procedures for the probability estimates of the matrix elements of the MPM, but some of them are still, in certain cases, rough approximations; for example, the collection of data in the field or the observations obtained in the laboratory frequently do not provide data associated with each individual in the population, and ad hoc assumptions have to be made to estimate MPM parameters, that may lead to biased results. Being these estimates so important to life history theory we here propose how to obtain unbiased estimates of MPM parameters when individuals are non-identifiable. The applicability of our approach is of importance for all those approaches of the life history theory field that depend upon demographic parameter estimates, particularly the determination of Darwinian fitness.

The parameters of the transition (**U**) and fertility (**F**) matrices must be correctly estimated for an MPM to be considered a good representation of the dynamics of a population. If the parameterization of an MPM (which requires the estimation of state survivorship and average state development time) are not reliable, they may well lead to biased models. Sometimes individuals can be identified (by marking individuals under field conditions or by the follow-up of individual cohort experiments) and thus the duration on every state can be easily estimated; but when individuals cannot be identified that estimation becomes problematic, and extremely difficult in the case of non-cohort data since the data have overlapping generations (Valpine et al., 2014).

It is very common to assign individuals to different classes, and during periodical observations these individuals will either survive, switch to another class or die. Here we present the theoretical background to build an MPM with the following very limited information at every observational period: (a) the number of individuals that died in every class, (b) the number of individuals that remained alive and moved (or not) to the next class, and (c) the total number of offspring produced in every class. This approach can also be used for non-cohort data (the transitions between classes are independent of the transitions between other classes), making it suitable for meta-analysis. In the rest of this paper, because of the kind of example used, we will refer to the "class" as stage, but if used with other type of organisms the more general term "state" would be applicable.

2. Parameter estimation for non-identifable, non-cohort data

A matrix model is composed of a matrix (**U**) of probabilities of transitions between stages, and a fertility matrix (**F**) (the reproductive effort per stage); for instance:

$$\mathbf{U} = \begin{pmatrix} P_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{pmatrix}$$

$$\mathbf{F} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 & f_7 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

Fig. 1 shows a diagram called "life cycle graph" corresponding to the example of the matrices **U** and **F** above. Dotted lines are customarily used to indicate reproduction, where we can see stage 7 is the only fertile class and newborns belong to stage 1.

Estimation of transition parameters MPM models depend on assumptions characteristic of Markovian models: the time spent by an individual in a particular stage i follows a Geometric distribution with parameter $1/(1-P_i)$, and, at any time unit, the probability that an individual in stage i dies in that stage or matures to stage $i+1$ are constant, with values R_i and G_i respectively. If at a given time t there are n_i individuals in some stage i, and one time unit later y_i individuals are dead and x_i individuals have graduated to next stage, we can estimate G_i and R_i with x_i/n_i and y_i/n_i respectively. By properties of Multinomial distributions (see Appendix 1):

$$E[x_i/n_i] = G_i, \qquad E[y_i/n_i] = R_i. \tag{1}$$

Since $P_i + G_i + R_i = 1$ we can be estimate P_i with $1 - x_i/n_i - y_i/n_i$. These estimates are based in n_i units of observation, where one unit of observation is defined as the fate of one individual in one unit of time.

In order to estimate P_i and G_i we do not need to follow up deaths and transitions to the next state at times $t, t+1, t+2, \ldots$, that is, we do not need to follow up a cohort in a time series: the memoryless property of Geometric distributions allows us to use the number of deaths and transitions from t to $t+1$ as a single, independent estimate based on the fate of n_i individuals. Of course, if one wishes to combine data from different experiments, the estimates obtained from some interval t to $t+1$ and the estimates obtained from another arbitrary t^* to t^*+1 can be combined, weighing the estimates according their own units of observation.

The estimates of G_i and R_i obtained over k (not necessarily adjacent) intervals are then:

$$\hat{G}_i = \frac{\sum^k x_i}{\sum^k n_i} \qquad \hat{R}_i = \frac{\sum^k y_i}{\sum^k n_i} \tag{2}$$

or,

$$\hat{R}_i = \frac{\text{Number of deaths observed in state } i}{\text{Total number of units of observation in state } i} \tag{3}$$

$$\hat{G}_i = \frac{\text{Number of 'graduations' observed in state } i}{\text{Total number of units of observation in state } i} \tag{4}$$

and

$$\hat{P}_i = 1 - \hat{R}_i - \hat{G}_i \tag{5}$$

Where, as before, y_i are those individuals found dead, and x_i are those individuals that have graduated to next stage. A formal derivation of these estimates and their properties is given in Appendix 1.

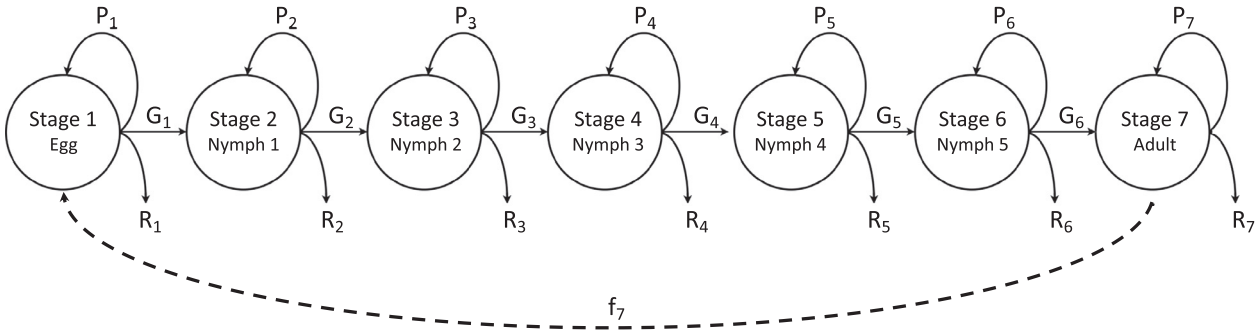

Fig. 1. An example life cycle graph with seven stages corresponding to the matrices **U** and **F**.

Table 1
Example of data set for N2 compartment.

Time unit (week)	Started the week	Died by the end of week	Graduated by the end of week
8	5	2	0
9	25	1	1
10	53	3	0
11	61	2	3
12	66	1	14
13	54	2	16
14	43	1	13
15	29	0	9
16	21	1	6
17	14	1	6
18	7	0	2
19	5	1	1
20	3	0	0
21	3	0	2
22	1	0	1
Sum	390	15	74

Estimation of fertility

In any MPM individuals in state i produces f_i offspring per unit time, and we only need to estimate the average offspring production per individual per unit of time, so the fertility of stage i is given by:

$$f_i = \frac{\text{Total offspring produced by individuals in state } i}{\text{Total units of observation in state } i}. \qquad (6)$$

3. Example

We provide an example of the estimation of P_i and G_i using data from the kissing bug *Eratyrus mucronatus* (Hemiptera, Triatominae), a potential vector of Chagas disease in Latin America (Rabinovich, J., unpublished data). The life cycle is divided in seven stages: the egg stage, five nymphal stages (N1–N5), and an adult stage, with one week as the time unit. In the laboratory, for every stage and every week, the following data was recorded:

- The number of individuals alive in each stage at the beginning of the time unit.
- The number of individuals that died in each stage by the end of the time unit.
- The number of individuals that graduated from one stage to the next by the end of the time unit.
- The number of eggs laid in each time unit for every stage.

Table 1 shows this kind of data for the Nymph 2 stage. For instance, Table 1 shows that at the beginning of week 12, there were 66 individuals, and that by the end of this week, one had died and 14 moved to the next stage (Nymph 3). The occasional increase of the number of individuals in the second column would indicate that individuals are entering this stage from the previous stage (Nymph 1). Using Eqs. (3)–(5) we obtain the following estimates of R_2, G_2 and P_2:

$$\hat{R_2} = \frac{\text{Total number of deaths observed in N2}}{\text{Total number of units of observation in N2}} = \frac{15}{390}$$

$$\hat{G_2} = \frac{\text{Total number of 'graduations' observed in N2}}{\text{Total number of units of observation in N2}} = \frac{74}{390}$$

thus:

$$\hat{P_2} = 1 - \hat{G_2} - \hat{R_2} = 301/390$$

We carried out the same calculations with the remaining stages (See Electronic Supplementary material) producing the population parameter estimates shown in Table 2. The last column is the estimate of the mean residence time.

Estimates (3)–(5) do not require weekly follow-up, that is, if the data for some weeks is lost, we still can use the rest of the data although the estimates would be based on fewer observations.

To calculate fertility, we use Eq. (6). As in this example there is only one reproductive stage (adults), and the total number of eggs laid was 5217, by dividing those 5217 eggs by the 2570 individual-weeks in the adult stage the fertility then is:

$$f_7 = \frac{5217}{2570} = 2.03 \ \text{ eggs individual}^{-1}\text{week}^{-1}$$

Once the **U** and **F** matrices have been estimated, we can evaluate the fitness of a population (See Caswell, 2001; 2009; Cochran and Ellner, 1992), as well as other life history traits (LHT) such as L, the longevity or the average lifespan; R_0, the basic reproductive number (the average offspring produced by an individual during its life); and several measures of generation time, for example: μ_1, average age of parents at which offspring is produced; $\bar{A}$, the average age of parents of offspring produced in one unit of time when the

Table 2
Estimates of the stage-specific demographic matrix parameters of the kissing bug *Eratyrus mucronatus*, from non-individualized cohorts reared in the laboratory at 16°C and 65% relative humidity (J. Rabinovich, unpublished data).

state	$\hat{G_i}$	$\hat{R_i}$	$\hat{P_i}$	$\hat{T_i}^{(*)}$
Egg	0.2080	0.0870	0.7050	3.390
N1	0.1330	0.0777	0.7892	4.744
N2	0.1897	0.0385	0.7718	4.382
N3	0.1288	0.0300	0.8412	6.297
N4	0.1269	0.0022	0.8710	7.752
N5	0.0603	0.0044	0.9353	15.456
Adult	0.0000	0.0214	0.9786	46.729

(*) Estimated with $\hat{T_i} = (1 - \hat{P_i})^{-1}$.

Table 3
Comparison of the main life history parameters estimated by the life table methodology using the FIFO rule and the procedure here proposed (MPM), for an experimental cohort of *E. mucronatus* initiated with 200 eggs (for the complete original data and the experimental conditions, see Electronic Supplementary Material). All time units in weeks.

Method	λ	r^*	R_0	μ_1	$\bar{A}$	$\bar{T}$	L
Life Table	1.050	0.048	26.085	71.781	62.815	66.813	30.750
MPM	1.058	0.056	26.085	87.749	44.695	58.358	30.750

(*) Population's finite growth rate ($e^r = \lambda$).

population has reached a stable state distribution; $\bar{T}$, the average time required for a population to increase by a factor of R_0. These life history traits can be calculated using the following expressions in matrix notation:

$$\begin{aligned} L &= \mathbf{1}'\mathbf{N}\mathbf{e_1} \qquad (\text{with } \mathbf{N} = (\mathbf{I}-\mathbf{U})^{-1}) \\ R_0 &= \mathbf{1}'\mathbf{F}\mathbf{N}\mathbf{e_1} \\ \mu_1 &= R_0^{-1}\mathbf{1}'\mathbf{F}\mathbf{N}\mathbf{U}\mathbf{N}\mathbf{e_1} + c \\ \bar{A} &= \mathbf{1}'\mathbf{F}\mathbf{M}\mathbf{V}\mathbf{M}\mathbf{e_1} + c \qquad (\text{with } \mathbf{V} = \lambda^{-1}\mathbf{U},\ \mathbf{M} = (\mathbf{I}-\mathbf{V})^{-1}) \\ \bar{T} &= \log R_0 / \log \lambda \end{aligned} \tag{7}$$

where λ = population growth rate per unit of time. That is, if $\mathbf{n}(t)$ is the total population size at time t, then $\mathbf{n}(t+1) = \lambda\ \mathbf{n}(t)$. In these equations, $\mathbf{1}$ is a column vector of ones, $\mathbf{e_1}$ is a column vector of zeros with a one in the first position and c is a constant indicating the average time in the interval [0,1] where births occur (Hernandez-Suarez, 2011). We use these expressions to construct Table 3.

How good are the LHT estimates in (7), themselves dependent on our proposed equations (2–6)? This is difficult to answer because the true LHT values are not known. The Life Table method provides, in theory, appropriate estimates of LHT if its underlying assumptions are met, which is rarely the case. This is so because the Life Table method requires an exact knowledge of the individuals that enter or leave a specific stage, which was not the case of the *E. mucronatus* cohort experiment. The Life Table in this example was constructed by assuming a FIFO (First In, First Out) rule which is customary in queuing theory. Under this rule the first individual that enters a stage is considered to be the first individual to leave that stage, allowing an estimate of the time an individual spends in each stage. This assumption is very difficult to be fulfilled for every stage in the life of an individual. Our contribution is precisely the proof that by handling the same recorded information in a different way, we can get rid of those stringent assumptions. If the assumptions of the Markov model are met, then, the estimates (3)-(5) are the best estimates of P_i, G_i and R_i we can get with the data, in the sense they are Uniformly Minimum Variance Unbiased Estimates (UMVUE) (see Appendix 1).

Table 3 shows that, in our example of the bug *E. mucronatus*, the largest differences between the calculated LHTs with each of the two method are related to the three measures of generation time (μ_1, $\bar{A}$ and $\bar{T}$), and we can only assume that this is a consequence of the FIFO assumption. Nevertheless, the LHTs related to population growth rates and longevity are highly similar between both methods.

As a robust control of the calculations by both methods note that the correct value of R_0 should be equal to the total number of laid eggs by the cohort divided by the initial number of eggs, 5217/200 = 26.08.

4. Discussion

Mathematical models should reproduce, as best as possible, the most important characteristics of the phenomena being modeled. Current procedures commonly used to parameterize matrix population models based on stage frequency data (i.e. with individuals that have not been identified) do not conform well with important observed life history traits, such as stage duration and stage survival. The basic discrepancy originates from the estimation of mean development time in every stage from external sources, frequently obtained under different conditions or from different seasons or environments. Thus, we discuss below in some detail the differences between our proposal and the current procedures to estimate MPM parameters; for the latter, we resort mainly to Caswell (2001).

We focus on the estimates of P_i, G_i and R_i by using the calculations suggested among others by Caswell (2001) using data from life table analysis; this method requires the calculation of the following parameters:

σ_i = probability of survival of an individual in stage i.

γ_i = fraction of the individuals in stage i that graduate to the next stage.

and then G_i and P_i are calculated as:

$$G_i = \sigma_i\gamma_i$$
$$P_i = \sigma_i(1-\gamma_i)$$

however, in order to calculate γ_i, we need an estimate of the average duration of stage i, T_i, so that a recursive approach in the parameters λ and γ_i is carried out in the following expression:

$$\gamma_i = \frac{(\sigma_i/\lambda)^{T_i} - (\sigma_i/\lambda)^{T_i-1}}{(\sigma_i/\lambda)^{T_i} - 1}$$

following Caswell (2001) definitions:

$$R_i = 1 - G_i - P_i = 1 - \sigma_i\gamma_i - \sigma_i(1-\gamma_i) = 1 - \sigma_i$$

therefore,

R_i = 1 − probability of survival of an individual in stage i

which implies that in the best scenario, Caswell (2001) approach will yield the same estimate for R_i than our estimate (3) as long as γ_i and T_i are adequately estimated. The proof that this extends to G_i and P_i is straightforward. In conclusion, our estimates (3)–(5) are not only useful when individuals are not identifiable, but are much simpler to calculate in comparison to Caswell (2001) method when individuals are identifiable. Another advantage of the procedure here proposed is that the average time in every state, T_i, is not required to estimate MPM parameters, but it is rather a by-product of the calculations as $\hat{T}_i = (1-P_i)^{-1}$.

Another classical method to parameterize a population model was suggested by Caswell and Twombly (1989) using the relationship:

$$[\mathbf{n}_{i-1}(t)\ \mathbf{n}_i(t)]\ \beta = \mathbf{n}_i(t+1)$$

where $\mathbf{n}_i(t)$ be a column vector containing the number of individuals in state i at time unit $t = 0, 1, 2, \ldots$ and vector $\beta = [G_{i-1}\ P_i]'$ and using regression estimators for β. This approach may lead to two serious problems: (a) the estimates of G_i and P_i may fall outside the range [0, 1], and (b) this approach does not weigh the estimates according to $n_i(t)$. In relation to the latter, consider a cohort where $n_1(t)$ is the number of individuals in the first stage at time t; since this number is non-increasing in time, the individuals in the first stage that move to the second stage at every time unit can be used to estimate G_1. Nevertheless, being a cohort, the estimates at earlier times (younger stages) always have more degrees of freedom than those at later times or stages. The regression approach does not weigh for the individual decreasing number with stages, whereas our suggested estimates (3)-(5) are in essence a weighting method. If the purpose is to parametrize an MPM, the procedure presented here is much simpler and requires less assumptions

than other methods that require the individual follow up of each organism until its death (Kiritani and Nakasuji, 1967; Manly, 1976) or that assumes that stage duration is known or estimated with no error (Yamamura, 1998) or depend upon other methods that require extremely complex calculations (Bellows and Birley, 1981; Iwasaki, 1996; Manly, 1997).

The use of the mean development time and not the mean residence time also impinges on the bias in current approaches to MPM?s parameterization; (Braner and Hairston (1989)) point out the important numerical differences that can sometimes result from using one or the other of these two measures. Once a life table has been constructed or the data compiled in the form of stage-frequency data, there is no algebraic procedure nor theory that can recover the development or the residence time by stages. Many efforts made to estimate average development times from stage-frequency data were based on some (frequently untested) assumptions; e.g., Fargo (1986) uses the FIFO assumption to cope with the lack of individual information. The procedure here proposed should be preferred over Fargo?s (1986) FIFO procedure, unless the FIFO assumption is valid, in which case that estimate and the one we here propose should be identical. As it is extremely exceptional to expect non-biased estimates of time-dependent parameters using the FIFO rule, we believe that our proposed procedure has various merits, which we can summarize as follows: (a) the parameterization of an MPM model provides MLE parameter estimates (see Appendix 1), (b) it does not require an individual follow-up of a cohort study, (c) it depends on the most simple information (usually recorded in most experimental cohort studies, as the one shown in Table 1 and exemplified in the electronic Supplementary Material), and (d) most important of all, our procedure is a novelty in that it does not require information on stage development (or stage residence) times, which current procedures require to be estimated externally, and represent a frequent source of error. Furthermore it provides a reliable estimate of the average residence time, given by $\hat{T}_i = (1 - P_i)^{-1}$. Thus, we expect that our proposed procedure will improve the estimation of the parameters of MPM models and facilitate their application to the various demographic and evolutionary fields of LHT theory.

Appendix

We propose a new procedure to estimate MPM parameters when individuals are non-identifiable, and without resorting to an estimate of developing time. Although the different moments of the parameters to be estimated can be obtained based on the statistical distribution of these parameters, in this Appendix we present the first two moments and show that, as derived from a multinomial distribution, the expected value and the variance of the MPM parameters are estimated by maximum likelihood.

Due to the memoryless property of Markov models an individual remains in a stage for a time that follows a Geometric distribution, and in every unit of time an individual in a particular stage is confronted to only one of three multiple exclusive events: to die (with probability R_i), to graduate to the next stage (with probability G_i), or to remain alive in the same stage (with probability P_i). The fraction of a cohort that materialized each of these events out of the total number of observations (n) for each stage, is the respective estimate of R_i, G_i and P_i, namely $\hat{R}_i$, $\hat{G}_i$ and $\hat{P}_i$, as shown in Table 1 for the 2nd stage of *E. mucronatus*. These estimates are estimates of a multinomial distribution with parameters n and R_i, G_i and P_i, and their distributional properties well known; for instance, $\hat{P}_i$ is the MLE of P_i, which is asymptotically normal with expected value P_i and variance $P_i(1 - P_i)/n$. Similarly for $\hat{G}_i$ and $\hat{R}_i$. It is also known the estimates are UMVUE.

A confidence interval of size $1 - \alpha$ for P_i is based on the asymptotic standard error of $\hat{P}_i$, and can be constructed as:

$$\hat{P}_i \pm Z_{1-\alpha}\left(\frac{\hat{P}_i(1-\hat{P}_i)}{n}\right)^{\frac{1}{2}}$$

where $Z_{1-\alpha}$ is a value such $P(Z > Z_{1-\alpha}) = \alpha/2$ where Z is a standard normal distribution. This is similar for $\hat{G}_i$ and $\hat{R}_i$. For details see Guttorp (1995), Theorem 2.16, p.65.

Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jtbi.2018.10.014.

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