

1 Persistent problems in the construction of matrix
2 population models

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11 **Abstract**

Matrix population models (MPMs) are powerful tools for translating demographic and life history information into a form that can be used to address a wide range of research topics, such as projecting population dynamics, evaluating stressor impacts on populations, and studying life history evolution. However, the reliability of such studies depends on the MPM being constructed in a way that accurately reflects the species' life history. We highlight three errors commonly encountered in published MPMs: (1) failing to include survival in the fertility coefficient; (2) introducing a one-year delay in age at first reproduction; and (3) incorrectly calculating the growth rate out of a stage class. We review the sources of such errors and provide new analyses revealing the impact of such errors on model predictions, using lionfish and American alligator models as examples. To quantify the prevalence of such errors we examined and scored the original publications underlying the models in the COMADRE Animal Matrix Database. The first two errors were found in 34% and 62%, respectively, of the published studies; nearly all were in models that used a “post-breeding census” representation of the life cycle (in which newborns—eggs, neonates, fledglings, etc.—are explicitly included). Of the studies where stages may last longer than one time step, 53% constructed the growth rate using inappropriate formulas for estimating the asymptotic population growth rate or its sensitivity to demographic parameters. These results suggest that further efforts may be required to educate biologists on the construction of MPMs, perhaps in concert with the development of new software tools. Furthermore, the conclusions of many studies that are based on MPMs may need to be re-examined, and synthetic

studies using the COMADRE Database need to be accompanied by careful examination of the underlying studies.

Key words: COMADRE Animal Matrix Database, Lefkovitch matrix, Leslie matrix, matrix population models, model construction, model validity

1. Introduction

The use of matrix population models (MPMs) for the ecological study of plants and animals has expanded rapidly in recent years (Salguero-Gómez et al., 2016, 2015). MPMs are a convenient way to synthesize demographic information about a population, and are useful in addressing ecological, evolutionary, and management questions (Caswell, 2001; Morris and Doak, 2002). Most early MPMs were developed by collaborations between biologists with expertise on the species at hand and modelers with deep understanding of the subtleties of modeling. MPMs now, having been long promoted as a straightforward translation of life-history information into quantitative analysis, are often being created by biologists who are primarily empirical ecologists or conservation biologists, and may have had little training in modeling beyond a graduate course in population ecology. One might then ask, do these MPMs reliably reproduce the life histories they are meant to represent?

It is important to remember that MPMs are approximations, both because they still abstract away much biological detail and because demographic measurements are imprecise. There are a variety of subtleties in constructing such models, especially when breeding is spread across a substantial fraction of the year or when there is substantial heterogeneity among individuals within an age or stage class; much theoretical work has gone into making MPMs more complex to account for this, and we are starting to better understand the effects of these phenomena on simple models (e.g., Fujiwara and Diaz-Lopez, 2017). But even setting aside these issues, we might hope that, if we assume that a simple life history description (e.g., as embodied in a life table or set of stage-based life-history parameters) is a useful description

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40 of the population, then the constructed MPM should accurately reproduce
41 that description. If it does not, then we are introducing additional errors
42 into the analysis above and beyond the inherent approximations of modeling.

43 One of us (Kendall) has spent two decades teaching MPMs to applied
44 masters students. This experience has revealed several aspects of MPM
45 construction that are particularly challenging to modelling novices, and thus
46 might be similarly challenging to biologists who do not regularly create
47 mathematical models of their system. At one level, the errors made by these
48 novices are “simply” accounting issues, but some students exhibit a strong
49 attachment to the incorrect formulations. We suspect that this difficulty,
50 for both students and researchers, is partly rooted in the contrast between
51 the often-loose way that terms are used to describe biological populations
52 and the very precise meanings of terms in MPMs (together with some
53 genuine linguistic ambiguity that plagues the field). However, some of these
54 issues may represent “threshold concepts” (Cousin, 2006) which, seeming to
55 violate common-sense intuition, are not easily learned through self-study of
56 a textbook.

57 We have not infrequently encountered published MPMs that embody
58 many the same mistakes made by Kendall’s students. Our goal in this
59 paper is to highlight these challenges (which are described in the next
60 section), quantify their impacts on the outputs of MPMs, and document their
61 prevalence in the peer-reviewed literature. We conclude with a discussion
62 of why these MPM construction errors are so prevalent, and how we might
63 improve future practice.

64 2. Challenges in MPM construction

65 We focus on animal population models in which the demography is
66 structured by age (Leslie matrices; Leslie, 1945) or developmental stage
67 (Lefkovitch matrices; Lefkovitch, 1965); plant and size structured models
68 present additional challenges, which would further complicate our presen-
69 tation. We also focus on species whose reproduction is concentrated in a
70 short breeding season (so-called “birth-pulse” populations; Caughley, 1967).
71 Many animal species satisfy this assumption, and this allows us to avoid the
72 extra complications associated with using discrete-time models to represent a
73 continuously breeding species. Note that by “breeding season” we mean the
74 season in which individuals are born or hatched, not the season during which
75 their parents mate. Age starts counting from birth, so that a reproductively
76 mature individual breeds on or about their birthday: e.g., if the age at first

Table 1: A sample table of demographic parameters for a species that reaches sexual maturity at age 3 (adult stage). Adults continue to survive and reproduce at successive ages with the same survival and birth rates. Note that, because we are using the stage-structured convention for assigning age class names (see text), the table may look slightly different from those in many textbooks.

Age in years (x)	Annual survival (σ_x)	Birth rate (b_x)	Stage
0	0.2	0	Newborn
1	0.4	0	Juvenile
2	0.4	0	Juvenile
3	0.9	3	Adult
4	0.9	3	Adult
\vdots	\vdots	\vdots	\vdots

77 reproduction is 5 years, then an individual has its first offspring on its fifth
78 birthday.

79 MPMs project the population from one nominal census date to the next.
80 While the census could, in principle, be at any time, in practice many MPMs
81 either census the population just before breeding (“prebreeding census”)
82 or just after breeding (“postbreeding census”). In a prebreeding census,
83 the youngest age class is made up of individuals all with age nearly one,
84 which we designate as age one. In a postbreeding census, the first age class
85 would comprise newborn individuals, all of age zero, the second class would
86 comprise individuals of age exactly one, etc. We refer to newborn individuals
87 with a subscript of zero; as a result, our postbreeding Leslie models will look
88 different from most textbooks, which assign newborns to “age class one” and
89 use a subscript of one.

90 2.1. Ensuring that the fertility coefficient spans a full timestep

91 In a table of demographic parameters (e.g., Table 1), age specific survival
92 and birth rates look as if they should make equivalent contributions to a
93 population model. But there is an important difference: survival (which we
94 denote σ_x for Leslie models and σ_i for Lefkovitch models, where x is the
95 age and i is the stage) represents the fraction of individuals in a class (x or
96 i) that survive for a full timestep, from time t to time $t + 1$. In contrast,
97 the birth rate (which we denote b_x for age-structured demography and b_i
98 for stage-structured demography) is an almost instantaneous event: it is
99 the average number of offspring produced at time t by an individual that

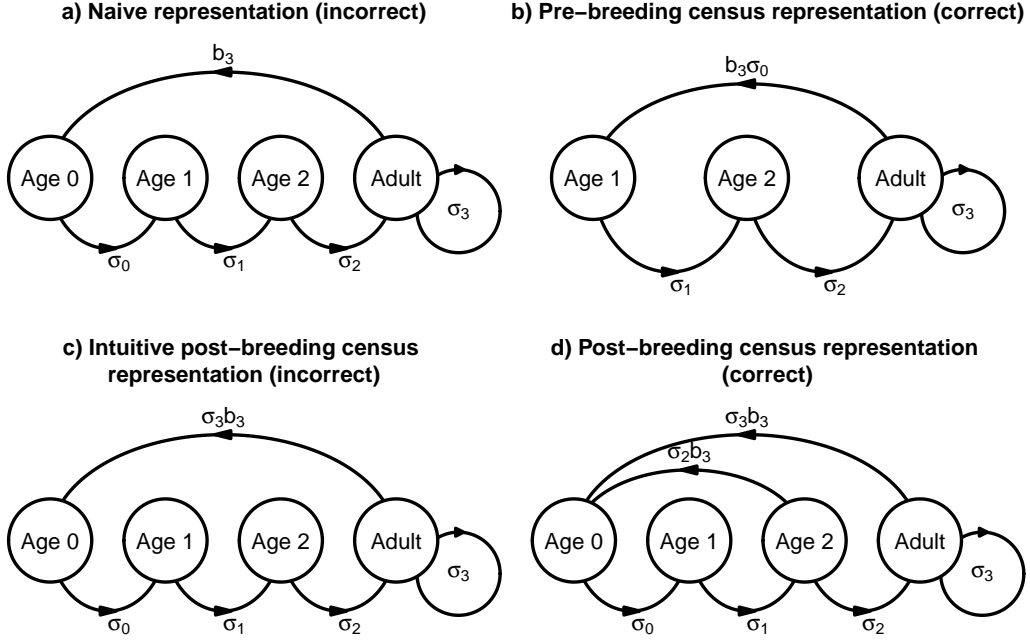


Figure 1: Four life cycle graphs that might (correctly or incorrectly) represent the demographic parameters in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the fertility coefficients must span a timestep and therefore include a survival term. (b) A pre-breeding census representation, in which the youngest censused class is Age 1 and the adult birth rate is multiplied by newborn survival. (c) An “intuitive” post-breeding census representation, in which the adult birth rate is correctly multiplied by adult survival, but which fails to account for the fact that Age 2 individuals will have reproduced (as adults) just prior to the next census. (d) A correct post-breeding census representation.

100 is alive at time t . It is tempting to draw a life cycle graph like the one in
 101 Fig. 1a (commonly seen in the literature). While this works as a *conceptual*
 102 diagram, translating it directly into an MPM by converting each arrow in
 103 the graph into a matrix element is incorrect: each element in the matrix
 104 must span a timestep, and b_x does not accomplish that.

105 To get the timestep into the fertility coefficient, b_x needs to be multiplied
 106 by a survival term—either that of the parent or of the offspring. Failing to
 107 include survival term will inflate the fertility coefficients. For a prebreeding
 108 census model, the fertility coefficient is $F_x = b_x \sigma_0$: the parent, in class x ,
 109 produces b_x offspring immediately after the census, and then these offspring
 110 survive to the end of the timestep at rate σ_0 —at which point they are age 1

(Fig. 1b). For an annual timestep, F_x represents the number of one-year-olds next year produced by an individual of age x this year.

In a postbreeding census, the parent (which will have just reproduced if it is already an adult) must survive for a timestep, aging by a timestep and possibly maturing into a new class, and then reproduces with a birth rate appropriate to its class at the end of the timestep. If we use x' to denote the parent's class at time $t + 1$, then the fertility coefficient is $F_x = \sigma_x b_{x'}$ (Fig. 1d). For an annual timestep, F_x is the number of zero-year-olds (newborns) produced next year by an individual that was in class x this year. Properly accounting for x' is a separate challenge that we address in the next subsection.

2.2. Matching the age at first reproduction to the species' life history

In an age-structured population, the lowest age with a non-zero birth rate represents the *age at first reproduction*; we will call that age x_m , for “age at [reproductive] maturity.” In a prebreeding census model (Fig. 1b), this does not present a conceptual challenge, as the newly matured, about-to-reproduce-for-the-first-time individuals are already classified as age x_m , matching intuition. However, in a post-breeding census model, the individuals who are age x_m at the end of the timestep, and have just reproduced for the first time, were age $x_m - 1$ at the beginning of the timestep. A model that has the first non-zero fertility coefficient associated with age x_m instead of $x_m - 1$ (Fig. 1c) results in the modeled age at first reproduction being $x_m + 1$, a year delay relative to the actual life history.

The solution is to add a fertility coefficient linking age class $x_m - 1$ to age class zero—the lower of the two fertility arrows in Fig. 1d. Embracing this fertility coefficient requires overcoming cognitive dissonance—“juveniles” are reproducing!—and we have found that students—and perhaps other nonmodellers—actively resist this.

An alternative approach for postbreeding census Leslie models is to change the indexing scheme, associating x with the individual's age at the *end* of the timestep (rather than the age at the beginning of the timestep, as we have done above). Then the individuals who will mature and reproduce before the next census are called age x_m , and their fertility is $F_{x_m} = \hat{\sigma}_{x_m} b_{x_m}$ (we use $\hat{\sigma}$ for survival to clarify that it is a differently indexed parameter from σ as used above). Thus, the cognitive dissonance is finessed by “hiding” the fact that these individuals started the timestep as juveniles. Indeed, many textbooks use this indexing convention for age-structured models. However, this alternative indexing convention cannot be maintained when moving

149 from age-structured to stage-structured models, as not all individuals that
150 start the timestep as juveniles will end it as adults.

151 So let us look at stage-structured models. The simplest stage-structured
152 model has newborns, a nonreproductive juvenile class that spans multiple
153 timesteps, and reproductive adults (Fig. 2). Within the juvenile class,
154 some individuals remain juveniles in the next timestep (should they survive;
155 Juvenile–Juvenile transition), whereas others mature into adults (Juvenile–
156 Adult transition). If γ_J is the fraction of surviving individuals that mature
157 (“grow”) at the end of the timestep, then the Juvenile–Juvenile transition
158 is given by $P_J = \sigma_J(1 - \gamma_J)$ and the Juvenile–Adult transition is given by
159 $G_J = \sigma_J\gamma_J$. We will treat the estimation of γ_J in the next section. As in
160 age-structured models, the fertility coefficient needs to include a survival
161 term, so Fig. 2a is incorrect. In a prebreeding census model, the adult birth
162 rate must be multiplied by newborn survival, and newborns removed from
163 the stage vector (Fig. 2b), whereas in a postbreeding census model, the
164 birth rate must be multiplied by the parent’s survival (Figs. 2c-d).

165 If the criterion for being classed as “adult” is that the individual can
166 reproduce, then just-matured adults should have non-zero fertility. In the
167 prebreeding census model (Fig. 2b), the individuals that have just matured
168 (made the transition from Juvenile to Adult) will reproduce at the beginning
169 of the next timestep. However, in the intuitive postbreeding census model
170 (Fig. 2c), the individuals that just matured won’t reproduce until the end
171 of the next timestep, a full timestep after their transition to adulthood.
172 In reality, the individuals that just made the Juvenile–Adult transition
173 were already adults at the just-passed breeding season, and hence have had
174 their first opportunity to reproduce. To represent this, we need a fertility
175 coefficient leading out of the juvenile class— $F_J = G_Jb_A$ (Fig. 2d)—which
176 again seems to defy common sense. This is particularly well illustrated in Fig.
177 7.3 of Mills (2007). Although this is the textbook solution, there a number
178 of other ways one might finesse this issue, such as classifying individuals as
179 adults at the beginning of the timestep in which they mature, or creating
180 a special “pre-adult” class between juveniles and adults. However, these
181 methods introduce additional complications such as giving the maturing
182 juveniles adult survival rather than juvenile survival (which might or might
183 not be desirable), or shortening the “juvenile” stage duration to account for
184 the extra stage.

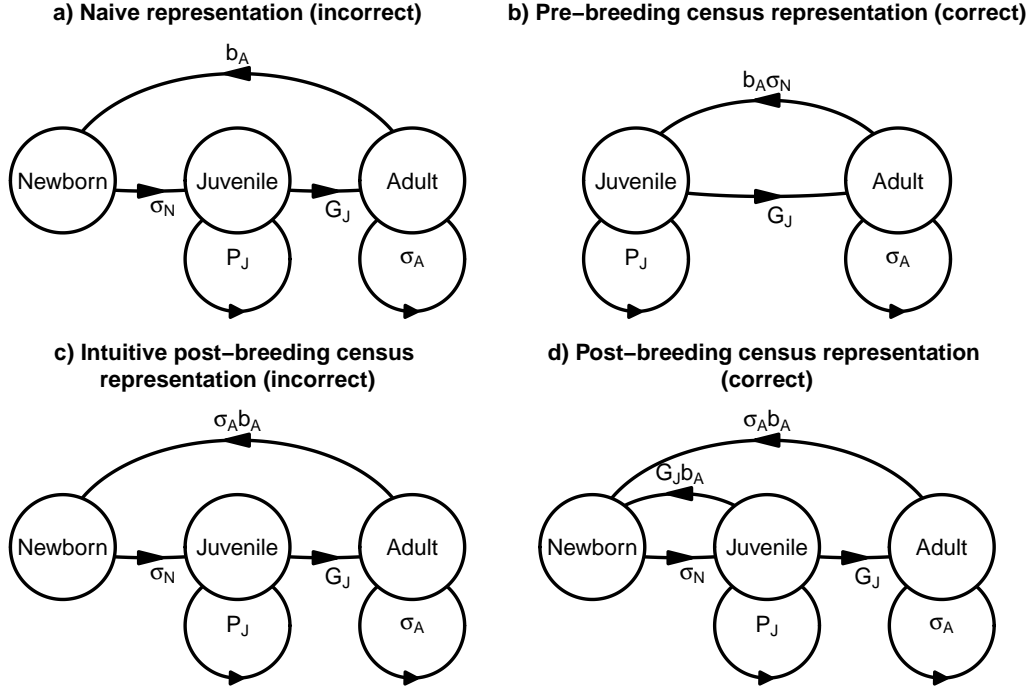


Figure 2: Four life cycle graphs that might (correctly or incorrectly) represent stage structured demographic parameters in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the fertility coefficients must span a timestep and therefore include a survival term. (b) A pre-breeding census representation, in which the youngest censused class is the juvenile stage and the adult birth rate is multiplied by newborn survival. (c) An “intuitive” post-breeding census representation, in which the adult birth rate is correctly multiplied by adult survival, but which fails to account for the fact that the maturing juveniles will have reproduced (as adults) just prior to the next census. (d) A correct post-breeding census representation.

2.3. Ensuring that the mean time in each developmental stage matches the species' life history

The final challenge is associated with estimating γ_x , the fraction of individuals growing (e.g., maturing) out of stage i . In many cases, the goal is to combine information on stage-specific survival, often variously collected, with knowledge about the stage duration (the number of timesteps that individuals remain in a stage before maturing). If stage durations are fixed (e.g., all individuals mature after two years as juveniles, as in Table 1), then the goal is to create a “stage-from-age” model (e.g., Ebert, 1998, Ch. 8) where the mean stage duration in the model equals the fixed stage duration in the life history. If the real stage durations are variable, then the goal is to create a model where the mean stage duration in the model equals the mean stage duration in the life history (in principle, the model should also match the variance in stage duration, but this seems never to be done in practice).

Caswell (2001) has a section of his book describing various ways of doing calculating γ_i to attain a specified stage duration, T_i . Depending on the species' life history, the stage duration might be fixed (all individuals mature after exactly T_i time steps in the stage) or variable (there is a distribution of times to complete the stage), in which case the mean stage duration needs to be calculated (this is not entirely straightforward, a topic we do not take up here). When the life history contains fixed stage durations, there is no single “best” approach, as the stage-structured model will never match the age-structured model completely. Nevertheless, the primary analyses performed on most published MPMs are to calculate the asymptotic growth rate (λ_1) and the sensitivity of λ_1 to underlying demographic parameters. For these calculations, there is one (and only one) recipe to create a stage-structured model that will, for any life history, generate the same results (at least to a very close approximation; we have not found theory on this) as the equivalent age-structured model with T_i age classes having the demography of stage i . As best we can tell, it was first introduced by Caswell (1989), although its first application to an ecological population may have been by Crowder et al. (1994).

The basic idea is that γ_i represents the fraction of individuals in the stage that have spent enough time in the stage to mature. This, in turn, depends on the (implicit) age structure within the stage. In general, this age structure could have any form, depending on the recent history of the population; the one well-defined case is when the population is at the stable age/stage distribution. This is exactly the condition under which λ_1 , the

Table 2: Three commonly used models for calculating γ_i , the fraction of individuals maturing from stage i , when the stage is meant to have a fixed stage duration T_i .

Maturation model	Fraction maturing from stage i (γ_i)
Asymptotic age-within-stage structure (AAS)	$\frac{(\sigma_i/\lambda_1)^{T_i-1}}{\sum_{j=0}^{T_i-1} (\sigma_i/\lambda_1)^j}$
Stationary age-within-stage structure (SAS)	$\frac{\sigma_i^{T_i-1}}{\sum_{j=0}^{T_i-1} \sigma_i^j}$
Flat age-within-stage structure (FAS)	$1/T_i$

asymptotic growth rate, is the observed population growth rate, $\lambda(t)$. Under this condition, there are two factors that affect the age distribution within the stage, and hence the fraction of individuals of an appropriate age to mature. The first is the stage-specific mortality, which determines how a cohort shrinks as it ages within the stage. The second is the asymptotic growth rate, which determines the degree to which a cohort entering from the previous stage in one year is larger or smaller than that of the previous year under the stable age or stage distribution. This makes γ_i non-trivial to calculate, as the resulting formula (Table 2) involves λ_1 , which can only be calculated once the MPM has been constructed and calibrated on data! The solution is an iterative approach: take an initial guess of λ_1 , calculate γ_i from the formula; calculate the dominant eigenvalue of the resulting matrix; use that as a new guess for λ_1 ; and repeat until the value of λ_1 stops changing. We will refer to this as the “asymptotic age-within-stage structure” (AAS) model.

The iterative nature of the AAS model may be daunting to non-modelers, especially those trained before the emergence of quantitative ecology using R. Such researchers may be tempted by easier-to-calculate formulas. Some discover a predecessor to the above Crowder et al. approach that appears in Crouse et al. (1987) (Table 2). This formula is complex-looking but straightforward to calculate, as it doesn’t require iteration (it incorporates the within-cohort dynamics, but *assumes* that $\lambda_1 = 1$). We will refer to this as the “stationary age-within-stage structure” (SAS) model (where “stationary” means that the population is neither growing nor declining).

Although we have seen no comment on this in the literature, the SAS model seems to be the correct choice when the goal is calculate statistics, such as the reproductive number (R_0), that involve following a cohort through the entire life cycle.

An even simpler approach is to say that, if the desired duration of stage i is T_i timesteps, then the fraction maturing is $1/T_i$ (Caswell, 2001). This relationship between the mean residence time (stage duration) and the fraction departing (maturing) is true for a simple Markovian departure process (e.g., Gallager, 1995). However, for the population process, different number of individuals are entering into the stage as a population may be growing or declining and individuals can also die before maturing. Consequently, this particular relationship between the mean duration and fraction maturing is correct under asymptotic conditions only if $\sigma_i/\lambda_1 = 1$. We will refer to this as the “flat age-within-stage structure” (FAS) model.

A rather different approach to estimating γ_i does not explicitly attempt to match the mean stage duration, but instead merely estimates γ_i as the observed fraction of surviving individuals in the stage that mature to the next stage. This requires repeated observations of marked individuals (capture histories), and might make use of tools such as multistate capture-mark-recapture models (e.g., Fujiwara and Caswell, 2001). As long as the modeled age-within-stage distribution remains the same as it was in the population during the observation period, then the model will get the mean stage duration correct. However, the estimated γ_i may be biased if the age-within-stage distribution changes unless the estimation process accounts for the age within stage of individuals. In particular, if γ_i is estimated by calculating the fraction of individuals in stage i that were observed to mature in a given year, the resulting model will accurately estimate λ_1 only if the observed population happened to be at the stable age structure. We will refer to this as the “observed age-within-stage structure” (OAS) model.

Among the AAS, SAS, and FAS models, only the AAS model will replicate λ_1 and its sensitivities from the fully age-structured model. Of course, a final approach, if the stage durations really are fixed, is to “unroll” the stage, replacing the single stage class with T_i age classes with identical survival coefficients (or, if the assumption of homogeneous survival within the stage was an approximation, with actual age-specific survival coefficients). After analysis, the age classes can be collapsed back to their stage to generate a stage structure or sensitivity analyses that are stage-specific rather than age-specific.

3. Consequences of incorrect MPM construction

We evaluate the impacts of these errors in MPM construction by examining several endpoints that many analyses focus on: the asymptotic population growth rate (λ_1), sensitivity analysis of λ_1 to changes in underlying vital rates, and life history statistics such as generation time. We approach this evaluation through theoretical analysis (where feasible and informative) and by examining two case studies: a lionfish (*Pterois* sp.) model with very high population growth (Morris et al., 2011) and a pair of American alligator (*Alligator mississippiensis*) models that project rapidly declining and nearly constant population dynamics (Dunham et al., 2014). These studies made all three of the errors described above; we singled them out not because they are particularly egregious (many other studies make these errors) but because the authors did an exceptional job of describing the species' life history, allowing us to infer the model they meant to construct. We started with the original matrices as "baseline" models, and constructed models that fixed various subsets of the focal errors to see how these errors affect the model projections and conclusions.

A matrix population model for lionfish was constructed by Morris et al. (2011) to investigate the potential approaches for controlling this invasive species. The modeled life history consisted of three stages (larvae, juvenile, and adult), and time step of the model was one month. The original model was a post-breeding census model, but it did not include the survival of adults in the fertility rate. The average duration of the juvenile stage was assumed to be 12 months in the model, and the fertility coefficient for juveniles was set to zero. This meant that the modeled lionfish take 14 months to reach first reproduction (one month in larval stage, 12 months in juvenile stage, and one additional month in fertility rate), in contrast to the target reproductive age of 12 months. The authors used the FAS model for calculating the transition rates for juveniles. We developed four stage-structured population models that gradually correct for some or all of these problems and three age-structured matrices, of which two include the original errors associated with the fertility coefficients (Appendix A). We used the eight models to calculate λ_1 , stable stage distribution, reproductive value, sensitivity and elasticity of λ_1 to stage-specific survival rate and fecundity, damping ratio, and generation time (Appendix A).

For the American alligator populations, Dunham et al. (2014) developed two stage-structured matrix population models to compare the status of northern and southern populations, which differed in stage durations and

birth rates. The original models consisted of five stages (eggs, larvae, juvenile, subadults, and adults), and the time step of the model was one year. Similarly to the lionfish model, the alligator models were post-breeding census models, but the authors did not include the survival of adults in the fertility rate. The first stage was egg stage, but it only lasted for three months; therefore, there was clear inconsistency in the time steps among stages. Dunham et al. (2014) used the AAS model to calculate transition rates for juvenile and subadult stages. We developed two additional stage-structured models that correct some or all of these problems and three age-structured matrices, of which two include the original errors associated with the fertility coefficients, for each population. The six population models for each population were used to calculate the same quantities that we calculated with the lionfish models (Appendix A).

3.1. Failure to include survival terms in the fertility coefficients

Failing to include survival terms in the fertility coefficients will make those coefficients too large (since survival is less than one). This will lead to an overestimate of λ_1 . This error most often occurs in postbreeding census models, and will be approximately

$$\mathcal{E}_{\text{surv}}(\lambda_1) \approx \sum_x (1 - \sigma_x) F_x S_{F_x},$$

where S_{F_x} is the sensitivity of λ_1 to the fertility coefficient F_x . Thus, if the survival terms are close to one (as they often are for adults) and the sensitivity of the asymptotic growth rate to survival is small (as it often is), then this error should generally be fairly small.

The fertility coefficients in both lionfish and alligator models in the original papers omitted the survival of adults. The effects of these errors can be observed by comparing the age-structured matrices with and without the correction (Appendix A). The first set of age-structured matrices (L6, A4, and A10) were converted from the original stage-structured matrices, which were missing the survival rate of adults. Another set of age-structured models (L8, A6, and A12) included corrected fertility coefficients with corresponding survival rates multiplied to the original fertility. When the survival rate was missing in the fertility coefficient, asymptotic population growth rate was always overestimated (Figs. A.1 and A.8), adult stable stage distribution was underestimated (Figs. A.2 and A.9), and adult reproductive value was overestimated (Figs. A.8 and A.16). The reduced adult stable stage distribution and increased adult reproductive value resulted from the fact the

models mistakenly assumed more offspring were born, inflating the number of younger individuals.

For both lionfish and alligator populations, the survival rate over the time step of a model was high (0.95 per month for lionfish and 0.83 per year for alligator). Therefore, the effects were relatively minor. However, when we deal with organisms with low adult survival rate or when the time step is extended (e.g. time step is changed to 1 year in the lionfish model), a fertility coefficient could be substantially inflated without adult survival rate being included, causing biases in demographic statistics.

3.2. Failure to allow individuals to reproduce when they first reach reproductive age

The failure to allow individuals to reproduce when they first reach reproductive age will have two consequences: R_0 , the net reproductive rate, will be reduced slightly; and the mean generation time, T_G , will be increased by a timestep. Both effects contribute to an underestimate of λ_1 ; the error is approximately

$$\mathcal{E}_{\text{mature}}(\lambda_1) \approx R_0^{1/T_G} - (\sigma_A R_0)^{1/(T_G+1)},$$

where σ_A is the one timestep survival of the newly matured class. This doesn't simplify easily, but it is clearly largest when the generation time is short or R_0 is large.

Both original lionfish and alligator models did not include a fertility coefficient associated with individuals transitioning into an adult stage. The effects of the missing fertility coefficient can be found by comparing models L2 and L3 (stage-structured lionfish models), L7 and L8 (age-structured lionfish models), A5 and A6 (age-structured alligator models for northern population), and A11 and A12 (age-structured alligator models for southern population). In all cases, the missing fertility coefficient caused the underestimation of asymptotic population growth rate (Figs. A.1 and A.8), overestimation of adult stage distribution (Figs. A.2 and A.9), and underestimation of adult reproductive value (Figs. A.3 and A.10).

The effects of the missing fertility coefficient depend on the life history strategy of organisms. For example, the effects were greater for the southern alligator population than northern alligator population because the duration from egg to adult stages was longer for northern population, causing fewer individuals to transition into adult stage each year, and the fecundity was lower for the northern population, causing fewer individuals to be born from

each parent. Both of these would cause the reproduction in the first year to be smaller, reducing the effects of the missing fertility coefficient to be small. The effects of the missing fertility coefficient is expected to be large for species for which the contribution of offspring from individuals reproducing the first time is large.

3.3. Failure to use AAS model for transition rate calculation

If the stage durations are fixed, such that a Leslie matrix model, with all age classes within the stage having the same survival, is the best model, then only the AAS stage-structured model will give the approximately correct λ_1 in general. The SAS model will be correct only if $\lambda_1 = 1$; if $\lambda_1 > 1$, then the maturation fraction will be too large and λ_1 will be overestimated; the opposite will be true if $\lambda_1 < 1$. Thus the SAS model will bias λ_1 away from one. The the bias from FAS model is similar, except that the critical value for λ_1 is σ_i . Thus, if there is more than one multi-timestep stage with different values of σ_i , and λ_1 is intermediate between these values, then the direction of bias introduced by the FAS model is unpredictable. The impact of using the observed transition rates is likely to be highly variable, depending on the nature of the deviations between the age structure when the population was observed and the asymptotic age structure.

The use of different maturation models (Table 2) has substantial effects on demographic statistics, and these effects can be observed by comparing the FAS (L3), SAS (L4), AAS (L5), and age-structured (L8) models for lionfish populations. The asymptotic population growth rate was substantially overestimated under the FAS and SAS models compared with the AAS and age-structured models (Fig. A.1), with latter two having the same growth rate estimate. Although the stable stage distributions of adults under the four models appear similar (Fig. A.2), the stable stage distributions of juveniles were underestimated with the FAS and SAS models compared with the age structured models (Fig. A.2), suggesting that the stable stage distribution of the larval stage was overestimated under the two stage-structured models. The reproductive value of adults were substantially underestimated with the FAS and SAS models compared with the AAS or age-structured models.

The original models for alligator populations used the SAS model (A2 and A8 for the northern and southern populations after correcting other problems). Therefore, we compared it with the AAS model (A3 and A9 for the northern and southern populations, respectively) and the age-structured model (A6 and A12 for the northern and southern populations, respectively). Similarly to the lionfish models, the AAS and age-structured models gave

the same asymptotic population growth rate. However, the SAS models underestimated the population growth rate for the northern population, and overestimated it for the southern populations. This resulted from the fact the estimated population growth rate was below 1 for the northern population and above 1 for the southern population. In other words, the SAS model magnified the deviation in asymptotic population growth rate from 1, as predicted by the theory above. When the asymptotic growth rate was less than 1, the SAS model also underestimated the adult stable stage distribution (Fig. A.9) and overestimated the adult reproductive value (Fig. A.10). The opposite effects were observed when the asymptotic growth rate was greater than 1.

3.4. *Effects on sensitivity, elasticity, damping ratio, and generation time*

As described above, the three common errors in constructing matrix population models can affect the population growth rate, stable stage distribution, and reproductive value, which are the three basic statistics associated with a population matrix. Calculating the sensitivity (or elasticity) of λ_1 to changes in matrix elements or underlying demographic parameters is often the primary goal of constructing an MPM, especially for management applications or studies of life history theory. Because the sensitivity and elasticity of the population growth rates to population parameters are functions of these basic statistics, they are also affected by the errors. Predicting the effects of MPM construction errors requires information about the second derivative of λ_1 with respect to model parameters (Caswell, 1996), the theory of which seems not to have been much developed. In a Lefkovich model, the second derivative of λ_1 with respect to diagonal matrix elements is positive, and with respect to off-diagonal elements seems to be generally negative (McCarthy et al., 2008). This suggests that overestimates of the maturation rate should reduce the sensitivity of λ_1 to both stasis and growth terms, thus reducing the overall sensitivity of λ_1 to survival. In addition, failing to include survival terms in the fertility coefficients will necessarily lead to underestimates of the sensitivity (and elasticity) of λ_1 to survival. For lionfish population, the rank order of both sensitivity and elasticity among stages changed from L3 to L4 as we changed the way we calculate the transition rates (Fig. A.6). This implies that conservation strategy can be affected by the errors in developing a population matrix.

There are a variety of ways to define generation time in demographic studies (Coale, 1972). In this study, we used the mean age of mothers to represent the generation time, applying formulas developed by Bienvenu and

469 Legendre (2015), which is a function of elasticity and fertility coefficients.
470 Therefore, any bias associated with these two quantities affects the estimated
471 generation time (Figs. A.7 and A.16). We found substantial and variable
472 impacts of MPM construction errors on the estimated generation time.
473 In addition, the estimated generation time tends to be biased with stage-
474 structured models (Fujiwara and Diaz-Lopez, 2017). These results suggest
475 that the calculation of generation time needs to be done carefully.

476 The damping ratio is given by $\lambda_1/|\lambda_2|$, where λ_1 is the eigenvalue of the
477 largest magnitude and λ_2 is that of the second largest, and it measures how
478 quickly transient dynamics dissipate over time. If λ_2 were not affected by the
479 errors in constructing population matrices, then the damping ratio and the
480 asymptotic population growth rate should correlate with each other. The
481 fact they deviate from each other (cf. Figs. A.1 and A.5, Figs. A.8 and A.15)
482 suggests the estimation of λ_2 is also affected by the errors in constructing
483 population matrices.

484 4. Prevalence of construction errors in published MPMs

485 4.1. Methods

486 To evaluate the prevalence of these errors in published MPMs, we exam-
487 ined a sample of the studies contained in the COMADRE animal matrix
488 model database (Salguero-Gómez et al., 2016). Using version 2.01 of the
489 database, we subset the data to studies of nonhuman animals that had a
490 DOI (as a simple filter to eliminate non-peer-reviewed studies). This left
491 65 studies published prior to the year 2000, and roughly twice that number
492 published from 2000 to 2018. We retained all of the 20th century studies
493 and took a random sample of 60 of the 21st century studies. Although
494 many studies publish multiple models, representing different sites or species,
495 we take the study as the unit of observation, as a similar approach was
496 usually taken in all the models within a publication. Some of the studies
497 did not actually contain MPMs (the models in the COMADRE database
498 were constructed by the COMADRE digitization team based on information
499 in the cited paper); we eliminated these.

500 Using a haphazard subset of studies, we developed a protocol to sys-
501 tematically assess each study (Appendix B). This protocol was applied by
502 3 members of the COMADRE digitization team, all graduate students in
503 demography at the Max Planck Institute for Demographic Research. After
504 initial training, consistency was ensured by having all members of the team,
505 as well as the lead author of this paper, independently apply the protocol to

the same set of papers until all were getting consistent results. If a question didn't apply (e.g., if it was not a stage-structure model), the answer was coded "NA;" if the answer could not be determined from the information in the publication, it was coded as "unknown."

We coded a model as a postbreeding census if the first age or stage class appeared to be newborn (e.g., eggs, neonates) or a small fraction of a timestep old (e.g., hatchlings, larvae, fledglings). We coded a model as a prebreeding census if the first age or stage class appeared to be one timestep old (e.g., yearlings, juveniles, 1-year-olds). While a number of other breeding models are possible, in practice nearly all models fell into one of these categories.

We examined the MPM to determine whether the fertility coefficients contained survival terms, and if so, whether they were appropriate to the model type. If the appropriate survival term was not present, we coded the model as "incorrect."

To identify the the first reproductive stage or age class, we examined quantitative (e.g., life table) or qualitative (e.g., text description of the life history) information about the species, as presented in the study. For postbreeding census models, we then asked whether the individuals maturing into that reproductive class had a nonzero fertility coefficient. Models lacking this fertility coefficient were coded as "incorrect."

For stage-structured models in which there was a target mean stage duration, we examined textual model descriptions and symbolic representations of the model to determine whether it was constructed using the AAS, SAS, FAS, or OAS formulations, or whether the stages were "unrolled" into a Leslie matrix formulation, with the implicit age-within-stage being made explicit. We examined the frequency of all formulations, and coded AAS and unrolled models as "correct" from the perspective of calculating the asymptotic growth rate, λ_1 .

For each of the three classes of errors, we calculated the overall percentage of relevant studies (i.e., studies that had a structure potentially subject to the error, and for which we could clearly determine how the model was constructed) that made that error. We also used logistic regression of error classification against publication year to examine whether these errors had become more or less frequent over time.

4.2. Results

The COMADRE Animal Matrix Database advertises itself as a repository of peer-reviewed published MPMs (Salguero-Gómez et al., 2016). Fine print

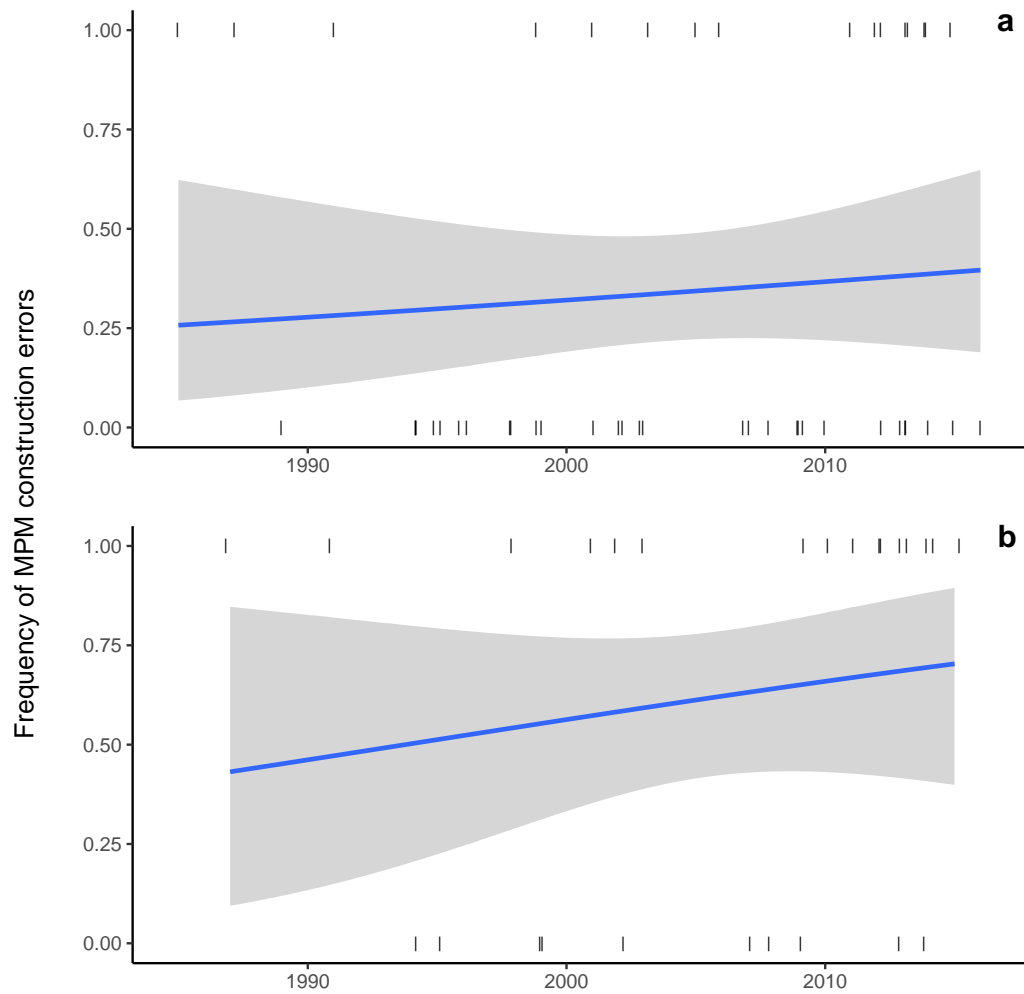


Figure 3: Trends in matrix population model construction errors through time. Trend line is logistic regression; vertical lines represent the data (jittered horizontally to prevent overlap). (a) Frequency of errors in the fertility coefficient, among all studies. (b) Frequency of errors in timing of first reproduction, among studies with post-breeding census models.

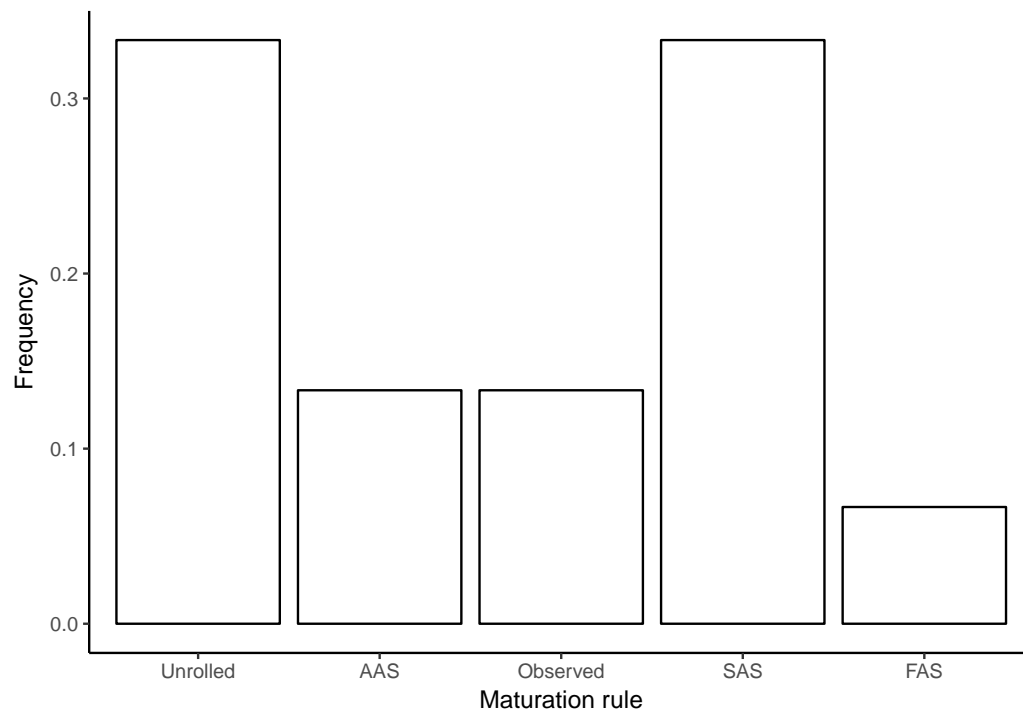


Figure 4: Frequency of approaches for setting maturation rates from stages with mean duration exceeding one timestep. See section 2.3 and Table 2 for descriptions of the approaches. Only the “Unrolled” and “AAS” approaches generate mean stage durations that match the target life history when the population is at the stable stage distribution.

in the user’s guide (Anonymous, 2017) reveals that, in some cases, the matrix does not actually appear in the cited paper, but was provided to the database as a personal communication. However, in the course of assessing articles from the database, we found many examples where the original publication did not construct an MPM. Instead, it appears that the database collators constructed MPMs from published demographic data, such as life tables. Since our goal was to assess the model construction accuracy of authors, not the database maintainers, we excluded these studies from our analysis. This removed 58 studies, leaving 67 for us to analyze.

We were able to unambiguously identify the components of the fecundity term in 47 studies. 34% of these studies failed to include an appropriate survival component in the fertility coefficients; 68.75% of these errors were in post-breeding census models. The frequency of these errors had no detectable trend over time ($P = 0.583$; Fig. 3a).

The potential for missing the reproductive event associated with first reaching reproductive age is only a feature of post-breeding census models. Of the 26 studies in which we could unambiguously determine both the last pre-reproductive stage or age class and in which we could identify fertility coefficients, 62% made this error. The frequency of these errors had no detectable trend over time ($P = 0.427$; Fig. 3b).

In our random sample, only 5 studies included models having at least one stage class that was meant to last for multiple timesteps. To obtain a reasonable sample size, we augmented this with the haphazard sample we had used to develop the evaluation protocol, which focused on stage structured models published since 2010. This led to 15 in which we were able to unambiguously classify the rule defining the maturation rate out of the stage(s); however, the date range was too narrow to evaluate trends through time. Of these, 53% did not use a rule that would generate a value of λ_1 that would match an age-structured model with the target mean stage duration (Fig. 4).

5. Discussion

We have described and analyzed three errors that are sometimes made when constructing animal matrix population models. These errors, involving the fertility coefficients and the maturation rates, cause the MPM to misrepresent the intended life history of the species. Based on our analysis of the COMADRE animal matrix model database (Salguero-Gómez et al., 2016), we find that these errors are quite common: 45% of the published

models that we evaluated have incorrect fertility coefficients (missing survival component, failure to reproduce upon maturation, or both). Furthermore, there is no evidence that these errors in the fertility coefficient are becoming less frequent through time (Fig. 3). Among the (admittedly small) sample of stage-structured models, fully half calculated the maturation rate in a way that would result in incorrect estimates of the asymptotic population growth rate.

These errors affect the value of quantities commonly calculated from MPMS, such as asymptotic growth rate and stage structure, elasticity analysis, generation time, and characteristics of transient dynamics. We can make a few generalizations about these effects. First, the two types of errors in the fertility coefficients have opposite effects on estimates of λ_1 , the asymptotic population growth rate. Second, incorrect specification of the maturation rate tends to have a larger impact on these statistics than do the other errors. Third, when the age at maturation is fixed (so that a Leslie model is the most appropriate representation) even a stage-structured model that correctly matches the mean time to maturity gives incorrect transient dynamics and generation time. Finally, most (but not all) of these errors are larger if λ_1 is far from one. However, in many cases we cannot yet predict either the direction or magnitude of biases introduced by the MPM construction errors. While a more complete understanding of these biases might be derived by analyzing more models, spanning a range of life histories, ecological understanding and management decisions would be better served by constructing the models correctly in the first place.

Why do these errors occur? The failure to include a survival component in the fertility coefficient is most surprising, as all textbooks make clear statements about the need for this. We suspect that the causes are threefold. First, different texts use different words to describe the birth rate (b_x)—e.g., the “maternity function”—and the fertility coefficient (F_x). For the latter, “fertility,” “fecundity,” and “reproduction” are used to represent F_x in different texts, and the terms have different scientific meanings in human demography and various fields of animal ecology. In particular, many animal ecologists use the term “fertility” to refer to the potential to have offspring, and so associate it with b_x rather than F_x (in contrast, demographers refer to this as “fecundity”). The use of a linguistically vague common language word to refer to a precisely defined model element creates the condition for nonmodellers to redefine the model element to match their understanding of the word, even when the textbook says otherwise. Second, the visual

619 similarity between the conceptual life cycle graph (Figs. 1a, 2a) and the
 620 life cycle graph that actually corresponds to the matrix may make it easy
 621 to forget to take the extra step of correctly formulating the fertility arrows.
 622 Finally, many nonmodellers seem to struggle to grasp the importance of
 623 having every transition in the MPM represent the same timestep. This may
 624 be a threshold concept, although students find it more to be unnecessary
 625 rather than counter-intuitive.

626 The need to include reproduction when an individual first matures, which
 627 is solely found in postbreeding census models, appears to be what education
 628 scholars call a “threshold concept:” an understanding that is essential to
 629 mastery of a field but that is troublesome to students because it appears to
 630 violate common sense intuition (Cousin, 2006; Meyer and Land, 2006). Here,
 631 the challenge is the intuition that no juveniles should have positive fertility
 632 coefficients. The challenge is probably exacerbated by the fact that most
 633 textbooks devote the most thorough explanation of MPM construction to
 634 age-structured models (where the confusing nature of postbreeding census
 635 models can be hidden by labeling an individual’s age class as its age at its
 636 *next* birthday). However, when these textbooks move to a (usually much
 637 briefer) description of stage-structured models, where this solution does not
 638 work, they generally switch notation without comment (a notable exception
 639 is Mills, 2007, who calls newborns “ N_{zero} ” for all models, and provides a
 640 very clear graphical depiction of both age-structured and stage-structured
 641 models).

642 The poor choice of maturation model is probably most easily understood.
 643 Most textbooks do not treat this issue, and those that do (e.g., Caswell,
 644 2001; Ebert, 1998) tend to be more mathematical than many nonmodellers
 645 may be comfortable with. Furthermore, they do not include clear guidance
 646 on which approach is most suitable for a given modeling objective.

647 How can the prevalence of these errors in MPM construction be reduced in
 648 the future? We have two pieces of advice to biologists seeking to construct an
 649 MPM for their species. First, we recommend that the model be constructed
 650 using the prebreeding framework. This reduces the likelihood of missing
 651 a survival term in the fecundity coefficient (as the newborn survival has
 652 to be put somewhere), and eliminates the nonintuitive fertility coefficients
 653 associated with transitions into reproductive classes. If a postbreeding
 654 census model is desired (e.g., so that model output can be compared with
 655 census data that includes newborns), then the prebreeding census model
 656 can be used to check the accuracy of the postbreeding census model (e.g.,

657 λ_1 should be identical for the two matrices), or emerging tools such as the
658 `pre_to_post` function in the **mpmtools** R package (Kendall, 2018) can be
659 used to do the conversion automatically.

660 Second, we recommend that, when the stage durations are fixed (all
661 individuals mature at the same age), the stage be “unrolled” into a Leslie
662 matrix model. This creates a model that makes correct projections under
663 both transient and asymptotic conditions, and can be used both for projecting
664 the population and for calculating life history statistics. This also allows
665 the demographic rates to vary with age within a stage (e.g., for species
666 such as fish with size-dependent demography), avoiding further pitfalls
667 highlighted by Fujiwara and Diaz-Lopez (2017). We recognize that in
668 long-lived species the results of sensitivity and elasticity analyses are often
669 more useful when aggregated by stage (Fujiwara and Diaz-Lopez, 2017); we
670 recommend performing this aggregation *after* analyzing the age-structured
671 model (e.g., by summing the elasticities associated with all the age classes
672 within a stage).

673 When the stage durations are not fixed, a more advanced solution is
674 to develop a model that incorporates both age and stage (Caswell et al.
675 (2018)). In this case, an accurate characterization of the distribution of stage
676 durations can be critical for many analytical outcomes, as described by de
677 Valpine et al. (2014) for continuous-time models. However, estimating the
678 parameter of such distributions can be challenging (see, e.g., the derivation
679 of parameters for time to next breeding in sea turtles by Ebert, 1998).

680 Experts can also help, by developing handbooks and training materials
681 that are both comprehensive and clear to non-modelers, who are experts
682 in biology and ecology but novices at modeling. The comprehensiveness
683 requires, in part, a thorough treatment of stage-structured models (which
684 are not described as completely as age-structured models in many texts), as
685 well as a comprehensive discussion of the consequences of various choices of
686 when the census should occur in the model. The clarity certainly requires
687 consistent notation and terminology, as well as attention to the knowledge
688 level of the audience, but that will probably not be sufficient. Educational
689 research suggests that when students arrive with misconceptions, clear and
690 accessible expositions of correct principles do not lead to learning, as the
691 students do not pay sufficient attention to recognize the difference between
692 the exposition and their prior belief; better learning occurs when they are
693 first presented with the misconception and then led to an understanding of
694 why it is wrong (Muller, Bewes, et al., 2008; Muller, Sharma, et al., 2008).

695 The biologically-based intuitions that underlay incorrect formulations of
696 MPMs may have the strength of scientific misconceptions, in which case
697 the training material will need to actively uproot them before a better
698 understanding of the model requirements can be learned.

699 Experts must also address the fact that many creators of animal MPMs
700 are not comfortable with even the simple programming required to calculate
701 quantities like the AAS maturation coefficient. While there are tools for
702 easing the *analysis* an MPM once the matrix has been constructed (e.g.,
703 Stubben and Milligan, 2007), little is available to help non-programmers
704 *construct* complex MPMs. A set of such tools, in a software environment with
705 which many ecologists are familiar, such as R, would be helpful, especially
706 in connection with a tutorial.

707 We have focused here on three particularly common errors in MPM
708 construction. However, other problematic errors may occur. For example,
709 nearly all animal MPMs are presented as birth-pulse models, but in some
710 cases reproduction is continuous over all or a significant fraction of the
711 model timestep. The lionfish model analyzed here illustrates this: lionfish
712 are described as laying a batch of eggs every 3 days, but by building a
713 birth-pulse model with a one-month timestep, Morris et al. (2011) fail
714 to account for the fact that the total monthly egg production is reduced
715 by parental mortality during the timestep, or by the fact that age classes
716 comprise a range of ages. Both of these issues are addressed by formulas
717 for birth-flow models, but such models are vanishingly rare in ecological
718 applications. Another challenge arises when demography is heterogeneous
719 within a stage class, as when individuals grow continuously through life
720 and survival and birth rates are size dependent. Fujiwara and Diaz-Lopez
721 (2017) have studied this and provide new recommendations for how best to
722 calculate “average” demographic rates within a heterogeneous stage class.

723 Plant MPMs, while prone to qualitatively similar types of errors, differ
724 in detail. In almost all cases, “newborns” are seeds; in many species,
725 newly produced seeds have the potential to transition to two qualitatively
726 different stages (seedlings and seed bank) in the following timestep. If the
727 fertility coefficient has seed production without subsequent seed survival
728 (and potential germination) then this creates the same error as we have
729 described here. Caswell (2001), in correcting his earlier teasel model (Werner
730 and Caswell, 1977) illustrates this issue; but he focuses not on the missing
731 survival term but on the fact that the error “introduced an unrealistic delay
732 of 1 year in the process of reproduction.” In our experience, it is often difficult

to determine whether a plant MPM has made this error, as the minimum time to germination is usually not described in the publication. In addition, most plant MPMs have at least some classes that are defined by size rather than stage. This creates a couple of challenges. First, an individual in a given size class can often transition to multiple other size classes, skipping a size class or even shrinking. In a postbreeding census model, this creates the need for complex fertility coefficients with a component for each of those transitions. Second, transition rates between size classes are usually estimated from the observed number of transitions; but the latter depend on the distributions of size within each size class (analogous to the distribution of age within stage discussed in the current paper), which in turn depend on the recent history of population fluctuations. The general solution for the latter problem is to avoid discrete size classes altogether and instead use an integral projection model (Ellner et al., 2016); but the creation of IPMs requires nontrivial programming skill.

In conclusion, we have found that errors in constructing animal population models are widespread, that these errors can have substantial quantitative (e.g., mis-estimation of the asymptotic growth rate, λ_1) and qualitative (e.g., mis-ranking the elasticity of λ_1 to various vital rates) consequences for the conclusions reached by the MPM analysis. This is bad news, and shows that we cannot count on peer review to ensure correct model construction. In some cases, the scientific conclusions or management recommendations supported by those models may be flawed. Furthermore, comparative studies that use the COMADRE database to obtain a “representative sample” of animal demography (e.g., Paniw et al., 2018) will be subject to extra “noise” (that may bias parameter estimates) unless erroneous models are corrected or excluded from the analysis. Fortunately, publications often contain enough life history information to allow the model to be revised to more closely match the species’ biology, allowing the conclusions of particular studies to be updated and comprehensive databases to be improved.

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