

# Persistent problems in the construction of matrix population models

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## 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 "postbreeding 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.

## 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; Salguero-Gómez and Plotkin, 2010). 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 of the population, then the

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

One of us (Kendall) has spent two decades teaching MPMs to applied masters students. This experience has revealed several aspects of MPM construction that are particularly challenging to modelling novices, and thus might be similarly challenging to biologists who do not regularly create mathematical models of their system. At one level, the errors made by these novices are “simply” accounting issues, but some students exhibit a strong attachment to the incorrect formulations. We suspect that this difficulty, for both students and researchers, is partly rooted in the contrast between the often-loose way that terms are used to describe biological populations and the very precise meanings of terms in MPMs (together with some genuine linguistic ambiguity that plagues the field). However, some of these issues may be instances of what education scholars call a “threshold concept”: an understanding that is essential to mastery of a field but that is troublesome to students because it appears to violate common sense intuition (Cousin, 2006; Meyer and Land, 2006).

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

## 2. Challenges in MPM construction

We focus on animal population models in which the demography is structured by age (Leslie matrices; Leslie, 1945) or developmental stage (Lefkovich matrices; Lefkovich, 1965); plant and size structured models present additional challenges, which would further complicate our presentation. We also focus on species whose reproduction is concentrated in a short breeding season (so-called “birth-pulse” populations; Caughley, 1967). Many animal species satisfy this assumption, and this allows us to avoid the extra complications associated with using discrete-time models to represent a continuously breeding species. Note that by “breeding season” we mean the season in which individuals are born or hatched, not the season during which their parents mate. Age starts counting from birth, so that a reproductively mature individual breeds on or about their birthday: e.g., if the age at first reproduction is 5 years, then an individual has its first offspring on its fifth birthday.

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

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

In a table of demographic parameters (e.g., Table 1), age specific survival and birth rates look as if they should make equivalent contributions to a population model. But there is an important difference: survival (which we denote  $\sigma_x$  for Leslie models and  $\sigma_i$  for Lefkovich models, where  $x$  is the age and  $i$  is the stage) represents the fraction of individuals in a class ( $x$  or  $i$ ) that survive for a full timestep, from time  $t$  to time  $t + 1$ . In contrast, the birth rate (which we denote  $b_x$  for age-

**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 ( $\sigma_x$ )	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
⋮	⋮	⋮	⋮

structured demography and  $b_i$  for stage-structured demography) is an almost instantaneous event: it is the average number of offspring produced at time  $t$  by an individual that is alive at time  $t$ . It is tempting to draw a life cycle graph like the one in Fig. 1a (commonly seen in the literature). While this works as a *conceptual* diagram, translating it directly into an MPM by converting each arrow in the graph into a matrix element is incorrect: each element in the matrix must span a timestep, and  $b_x$  does not accomplish that.

To get the timestep into the fertility coefficient,  $b_x$  needs to be multiplied by a survival term—either that of the parent or of the offspring. Failing to include survival term will inflate the fertility coefficients. For a prebreeding census model, the fertility coefficient is  $F_x = b_x \sigma_0$ : the parent, in class  $x$ , produces  $b_x$  offspring immediately after the census, and then these offspring survive to the end of the timestep at rate  $\sigma_0$ —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 postbreeding 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

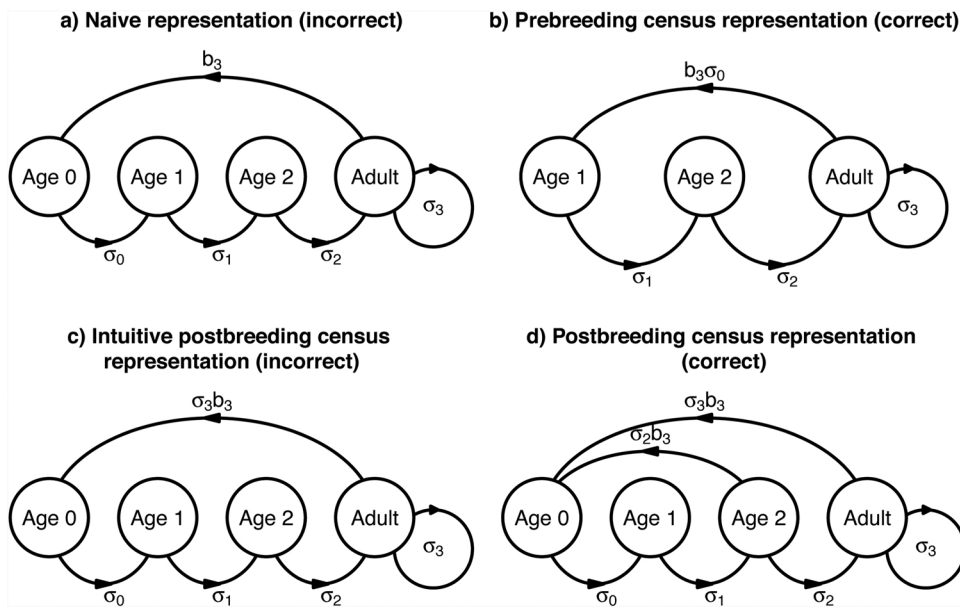


Fig. 1. Four life cycle graphs that might (correctly or incorrectly) represent the demographic parameters in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the fertility coefficients must span a timestep and therefore include a survival term. (b) A prebreeding census representation, in which the youngest censused class is Age 1 and the adult birth rate is multiplied by newborn survival. (c) An “intuitive” postbreeding 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 postbreeding census representation.

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

So let us look at stage-structured models. The simplest stage-structured model has newborns, a nonreproductive juvenile class that spans multiple timesteps, and reproductive adults (Fig. 2). Within the juvenile class, some individuals remain juveniles in the next timestep (should they survive; Juvenile–Juvenile transition), whereas others mature into adults (Juvenile–Adult transition). If  $\gamma_J$  is the fraction of surviving individuals that mature (“grow”) at the end of the timestep, then the Juvenile–Juvenile transition is given by  $P_J = \sigma_J(1 - \gamma_J)$  and the Juvenile–Adult transition is given by  $G_J = \sigma_J\gamma_J$ . We will treat the estimation

of  $\gamma_J$  in the next section. As in age-structured models, the fertility coefficient needs to include a survival term, so Fig. 2a is incorrect. In a prebreeding census model, the adult birth rate must be multiplied by newborn survival, and newborns removed from the stage vector (Fig. 2b), whereas in a postbreeding census model, the birth rate must be multiplied by the parent’s survival (Figs. 2c–d).

If the criterion for being classed as “adult” is that the individual can reproduce, then just-matured adults should have non-zero fertility. In the prebreeding census model (Fig. 2b), the individuals that have just matured (made the transition from Juvenile to Adult) will reproduce at the beginning of the next timestep. However, in the intuitive postbreeding census model (Fig. 2c), the individuals that just matured won’t reproduce until the end of the next timestep, a full timestep after their transition to adulthood. In reality, the individuals that just made the Juvenile–Adult transition were already adults at the just-passed breeding season, and hence have had their first opportunity to reproduce. To represent this, we need a fertility coefficient leading out of

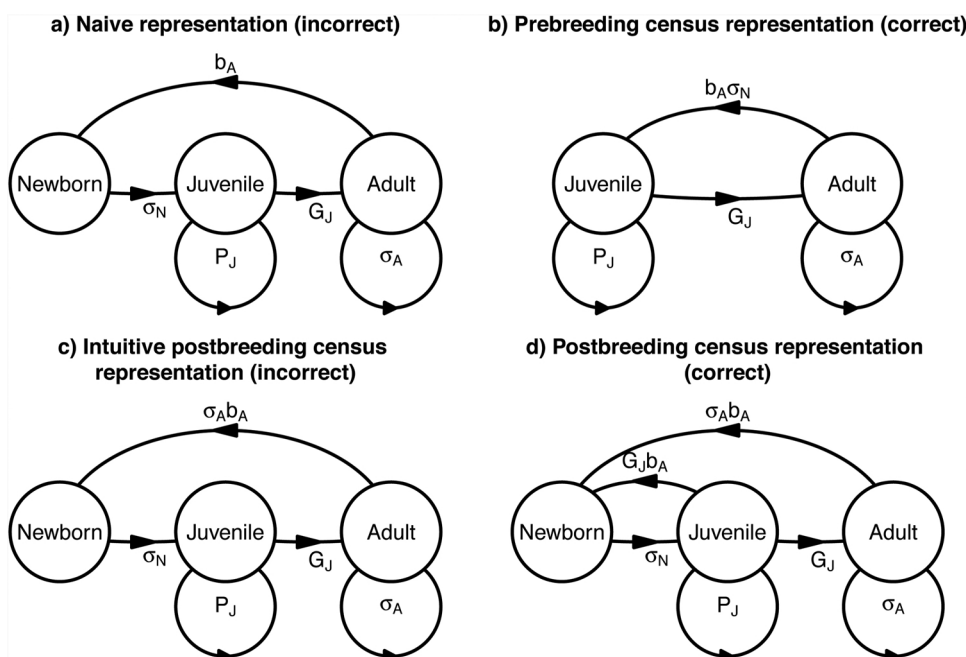


Fig. 2. Four life cycle graphs that might (correctly or incorrectly) represent stage structured demographic parameters in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the fertility coefficients must span a timestep and therefore include a survival term. (b) A prebreeding 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” postbreeding 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 postbreeding census representation.

the juvenile class— $F_j = G_j b_A$  (Fig. 2d)—which again seems to defy common sense. This is particularly well illustrated in Fig. 6.3 of Mills, 2013; Fig. 7.3 in the 2007 first edition). Although this is the textbook solution, there are a number of other ways one might finesse this issue, such as classifying individuals as adults at the beginning of the timestep in which they mature, or creating a special “pre-adult” class between juveniles and adults. However, these methods introduce additional complications such as giving the maturing juveniles adult survival rather than juvenile survival (which might or might not be desirable), or shortening the “juvenile” stage duration to account for the extra stage.

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

The final challenge is associated with estimating  $\gamma_i$ , 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  $\gamma_i$  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 ( $\lambda_1$ ) and the sensitivity of  $\lambda_1$  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  $\gamma_i$  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  $\lambda_1$ , the 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  $\gamma_i$  non-trivial to calculate, as the resulting formula (Table 2) involves  $\lambda_1$ , which can only be calculated once the MPM has been parameterized! The solution is an iterative approach: take an initial guess of  $\lambda_1$ , calculate  $\gamma_i$  from the formula; calculate the dominant eigenvalue of the resulting matrix; use that as a new guess for  $\lambda_1$ ; and repeat until the value of  $\lambda_1$  stops changing. We will refer to this

**Table 2**

Three commonly used models for calculating  $\gamma_i$ , 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 $i$ ( $\gamma_i$ )
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)	$1/T_i$

as the “asymptotic age-within-stage structure” (AAS) model.

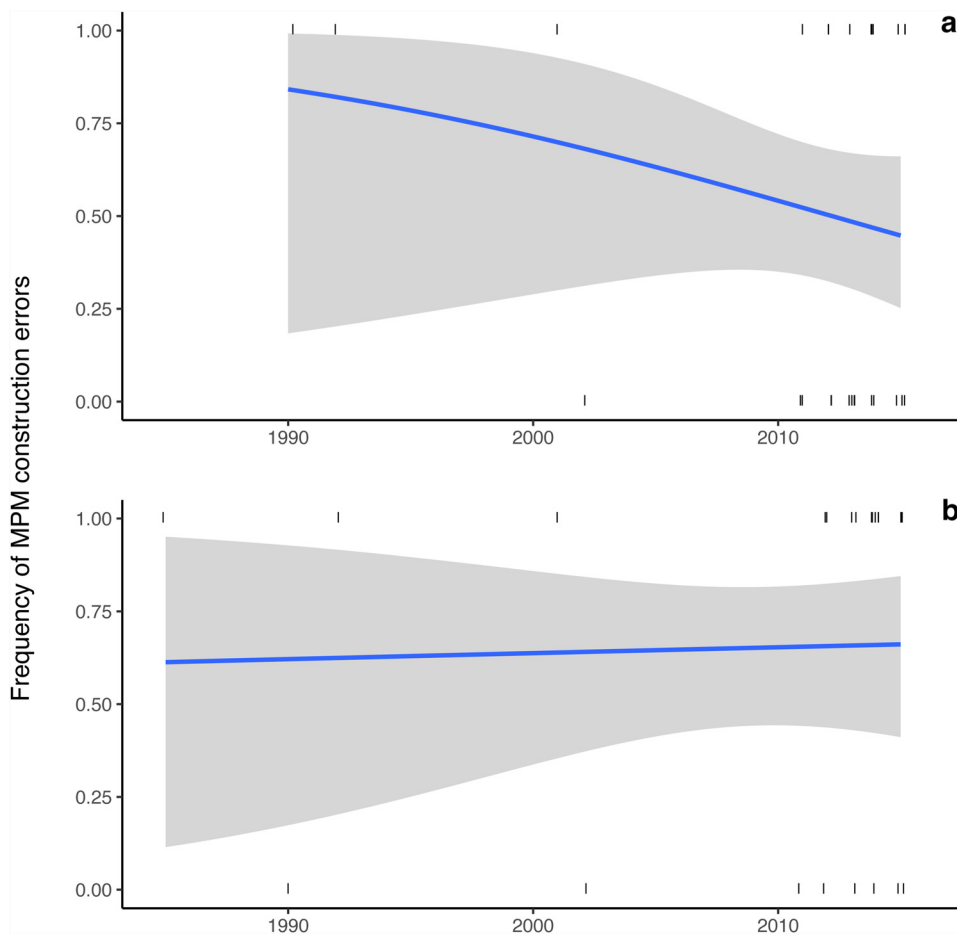
The iterative nature of the AAS model may be daunting to non-modelers, especially those trained before the emergence of quantitative ecology using R. Such researchers may be tempted by easier-to-calculate formulas. Some discover a predecessor to the above Crowder et al. approach that appears in Crouse 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 to 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., Gallagher, 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  $\gamma_i$  does not explicitly attempt to match the mean stage duration, but instead merely estimates  $\gamma_i$  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  $\gamma_i$  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  $\gamma_i$  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  $\lambda_1$  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  $\lambda_1$  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.





**Fig. 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 postbreeding census models.

### 3. Prevalence of construction errors in published MPMs

#### 3.1. Methods

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

Using a haphazard subset of studies, we developed a protocol to systematically assess each study (Appendix B). This protocol was applied by 4 of the authors. After initial training, consistency was ensured by having all assessors 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 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,  $\lambda_1$ .

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.

### 3.2. Results

The COMADRE Animal Matrix Database advertises itself as a repository of peer-reviewed published MPMs (Salguero-Gómez et al., 2016). Fine print 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 at all. 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 30 studies. 53% of these studies failed to include an appropriate survival component in the fertility coefficients; 100% of these errors were in postbreeding census models. The frequency of these errors had no detectable trend over time ( $P = 0.198$ ; Fig. 3a).

The potential for missing the reproductive event associated with first reaching reproductive age is only a feature of postbreeding census models. Of the 24 studies in which we could unambiguously determine both the last pre-reproductive stage or age class and in which we could identify fertility coefficients, 67% made this error. The frequency of these errors had no detectable trend over time ( $P = 0.755$ ; Fig. 3b).

In our random sample, only 19 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 14 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, 64% did not use a rule that would generate a value of  $\lambda_1$  that would match an age-structured model with the target mean stage duration (Fig. 4).

### 4. Consequences of incorrect MPM construction

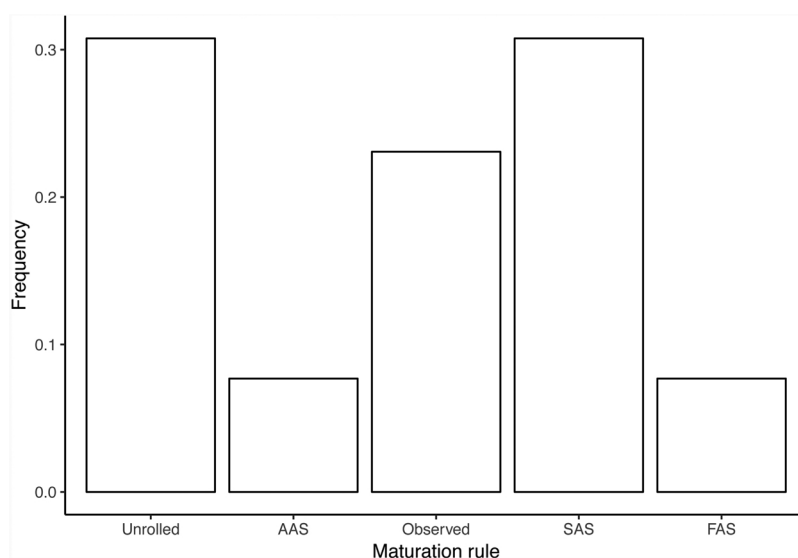
We evaluate the impacts of these errors in MPM construction by examining several endpoints that many analyses focus on: the asymptotic population growth rate ( $\lambda_1$ ), sensitivity analysis of  $\lambda_1$  to changes in underlying vital rates, and life history statistics such as generation time. 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 first focus on the effects on  $\lambda_1$  and then evaluate the effects on other endpoints.

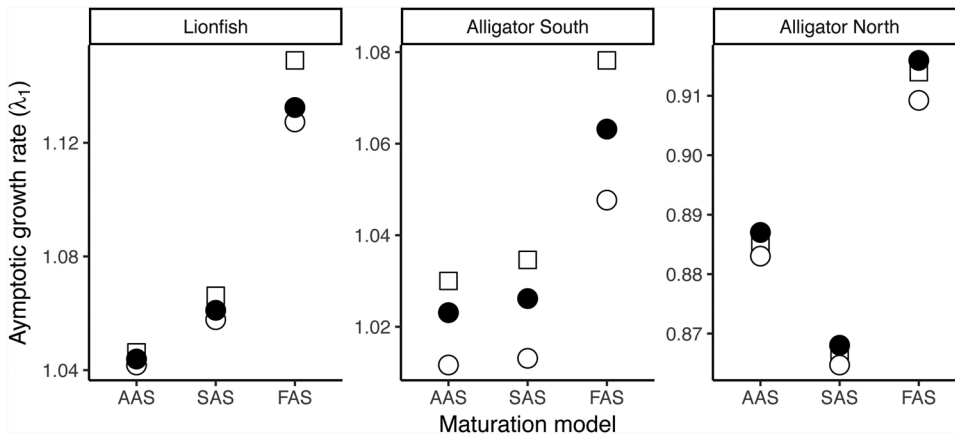
A matrix population model for lionfish was constructed by Morris et al. (2011) to investigate the potential approaches for controlling this invasive species. The modeled life history consisted of three stages (larvae, juvenile, and adult), and time step of the model was one month. The original model was a postbreeding 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. The full model is described (as model L1) in 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 postbreeding 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 SAS model to calculate transition rates for juvenile and subadult stages. The full models are described (as models AN1 and AS1) in Appendix A.

In order to investigate the effects of the errors on  $\lambda_1$  with the lionfish and American alligator matrices, we constructed stage structured population matrices that corrected the three types of errors (models L5, AN3, and AS3 in Appendix A). Then, we systematically inserted the errors back to the model and developed the total of nine models for comparison. These models vary in maturation models (AAS, SAS, FAS) and the presence or absence of reproduction by maturing juveniles (with adult survival in the fertility coefficient). When the reproduction by maturing juveniles was absent, we also allowed adult survival in the



**Fig. 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.



**Fig. 5.** Asymptotic growth rate ( $\lambda_1$ ) for various prebreeding census MPMs of the lionfish and alligator populations. Factors varied include three maturation models (AAS, SAS, FAS), the presence (squares) or absence (circles) of reproduction by maturing juveniles, and the presence (open symbols) or absence (filled symbols) of adult survival included in the fertility coefficient. The correct model is the open square with the AAS maturation model.

fertility coefficient to be absent.

#### 4.1. 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  $\lambda_1$ . 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  $\lambda_1$  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 open (with survival) and filled (without survival) circles in Fig. 5. When the survival rate was missing in the fertility coefficient, asymptotic population growth rate was always overestimated. 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. the 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. The effect was slightly higher for the southern population of American alligator than the northern population. This resulted from a larger fecundity associated with the southern population (5.98 individuals per year) compared with the northern population (2.37 individuals per year), suggesting the error may be magnified for organisms with high fecundity.

#### 4.2. 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  $\lambda_1$ ; 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  $\sigma_A$  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.

The original lionfish and alligator models did not include a fertility

coefficient associated with individuals transitioning into an adult stage. In all cases, the missing fertility coefficient caused an underestimation of the asymptotic population growth rate. The effects of the missing fertility coefficient depend on the life history strategy of the organisms. For example, the effects were greater for the southern alligator population than northern alligator population (compare open circles and squares in Fig. 5) because the southern population had a shorter duration from egg to adult stages (resulting in smaller generation time) and higher birth rate (resulting in higher  $R_0$ ) than the northern population. 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.

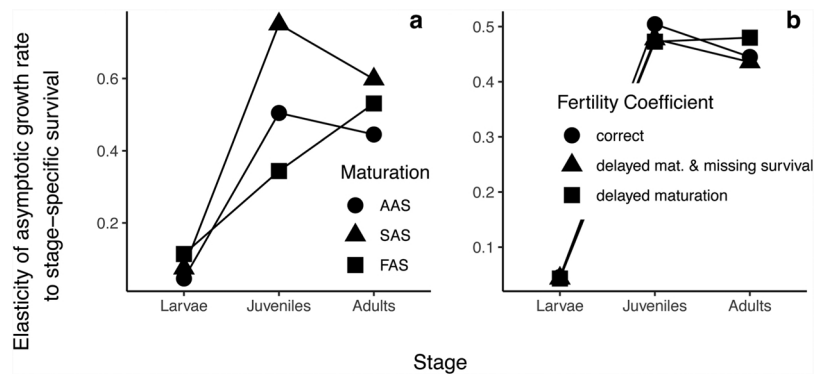
#### 4.3. Failure to use AAS model for transition rate calculation

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  $\lambda_1$  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  $\lambda_1$  will be overestimated; the opposite will be true if  $\lambda_1 < 1$ . Thus the SAS model will bias  $\lambda_1$  away from one. The bias from FAS model is similar, except that the critical value for  $\lambda_1$  is  $\sigma_i$ . Thus, if there is more than one multi-timestep stage with different values of  $\sigma_i$ , and  $\lambda_1$  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  $\lambda_1$  (Fig. 5). In particular, the asymptotic population growth rate was substantially overestimated under the FAS models compared with the AAS models. On the other hand, SAS models overestimated  $\lambda_1$  when  $\lambda_1 > 1$  (lionfish and southern population of American alligator) compared with AAS models, but it underestimated when  $\lambda_1 < 1$  (northern population of American alligator). In general, the SAS model magnifies the deviation in asymptotic population growth rate from 1, as predicted by the theory above.

#### 4.4. Effects of errors on sensitivity and elasticity analysis

A common goal of constructing a matrix population model is to examine the sensitivity or elasticity of  $\lambda_1$  to underlying demographic parameters, often in the service of informing population management or understanding life history evolution. Predicting the effects of MPM construction errors on these quantities requires information about the



**Fig. 6.** Effects of MPM construction errors on the elasticity of  $\lambda_1$  to stage-specific survival in the lionfish model. (a) Contrasts among the three maturation models, using correct values for the fertility coefficients. (b) Contrasts between approaches to fertility coefficient construction, using the (correct) AAS maturation model.

second derivative of  $\lambda_1$  with respect to model parameters (Caswell, 1996), the theory of which seems to only have been developed for Lefkovich models. In a Lefkovich model, the second derivative of  $\lambda_1$  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  $\lambda_1$  to both stasis and growth terms, thus reducing the overall sensitivity of  $\lambda_1$  to survival. In addition, failing to include survival terms in the fertility coefficients will necessarily lead to underestimates of the sensitivity (and elasticity) of  $\lambda_1$  to survival.

To look at the specific effects on elasticities to particular parameters, we calculated the elasticities of  $\lambda_1$  to stage-specific survival across the same suite of error combinations as we did for  $\lambda_1$ . For the lionfish population, the choice of maturation model had a substantial impact on the elasticity of  $\lambda_1$  to juvenile survival, and the rank order of elasticities to juvenile and adult survival was reversed by the FAS model (Fig. 6a). The impacts of errors in the fertility coefficients had a very modest impact on elasticities (Fig. 6b). In contrast, the elasticities of  $\lambda_1$  to stage-specific survival in the alligator populations were nearly unaffected by any of the matrix construction errors (results not shown).

#### 4.5. Effects of errors on other endpoints

As described above, the three common errors in constructing matrix population models can affect the population growth rate. However, calculating other endpoints such as stable stage distribution, reproductive value, sensitivity, elasticity, generation time, and damping ratio are often the primary goal of constructing an MPM, especially for management applications or studies of life history theory. Here, we investigate the effects of the errors on these endpoints using matrices for the lionfish and two populations of American alligators.

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. For the lionfish population, we developed four stage-structured population models that gradually correct for some or all of the problems and three age-structured matrices, of which two include the original errors associated with the fertility coefficients (Appendix A). For the American alligator populations, we developed two additional stage-structured models that correct some or all of the problems and three age-structured matrices, of which two include the original errors associated with the fertility coefficients, for each population. All of these models were used to calculate  $\lambda_1$ , stable stage distribution, reproductive value, sensitivity and elasticity of  $\lambda_1$  to stage-specific survival rate and fecundity, damping ratio, and generation time. The full results are shown in Appendix A; here, we highlight some of the key outcomes.

The effects of failure to include survival terms in the fertility coefficients can be observed by comparing the age-structured matrices with and without the correction. The first set of age-structured matrices (L6,

AN4, AS4) included corrected fertility coefficients with corresponding survival rates multiplied to the original fertility. When the survival rate was missing in the fertility coefficient, then the adult proportion of the stable stage distribution was underestimated (Figs. A.2. and A.9) and the adult reproductive value was overestimated (Figs. A.8 and A.16). These effects resulted from the fact the models mistakenly assumed more offspring were born, inflating the number of younger individuals.

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), AN5 and AN6 (age-structured alligator models for northern population), and AS5 and AS6 (age-structured alligator models for southern population). In all cases, the missing fertility coefficient caused an overestimation of the adult proportion of the stable stage distribution (Figs. A.2 and A.9) and an underestimation of adult reproductive value (Figs. A.3 and A.10).

The effects of using different maturation models can be observed by comparing the FAS (L3), SAS (L4), AAS (L5), and age-structured (L8) models for lionfish populations. Although the stable stage distributions of adults under the four models appear similar (Fig. A.2), the juvenile proportion in the stable stage distributions were underestimated with the FAS and SAS models compared with the age structured models (Fig. A.2). The reproductive value of adults were substantially underestimated with the FAS and SAS models compared with the AAS or age-structured models.

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

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

## 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: 60% 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  $\lambda_1$ , 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  $\lambda_1$  is far from one.

Nevertheless, the case studies we analyzed suggest that many analyses conducted with flawed MPMs may have broad validity. For example, in none of the case studies did the errors introduce misclassifications of population decline versus increase. Furthermore, errors in  $\lambda_1$  are generally modest, except when an inappropriate maturation model is used (Fig. 5). Finally, the rank orders in stage-specific values in the stable stage and reproductive value distributions were unaffected by the matrix construction errors. However, we have only a limited sample of case studies, and for some outcomes even this small sample gives inconsistent results for the direction or magnitude of biases introduced by the MPM construction errors. For example, the rank order of the elasticities of  $\lambda_1$  to the vital rates might (alligator) or might not (lionfish) be robust to model 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 similarity between the conceptual life cycle graph (Figs. 1a, 2a) and the life cycle graph that actually corresponds to the matrix may make it easy to forget to take the extra step of correctly formulating the fertility arrows. Finally, many nonmodellers seem to struggle to grasp the importance of having every transition in the MPM represent the same timestep. This may be a threshold concept (i.e., an idea that is essential to mastery of a field but that is troublesome to students because it appears to violate common sense intuition; Cousin, 2006; Meyer and Land, 2006), although students find it more to be unnecessary rather than counter-intuitive.

The need to include reproduction when an individual first matures, which is solely found in postbreeding census models, seems to be a clear example of a threshold concept. Here, the challenge is the intuition that no juveniles should have positive fertility coefficients. The challenge is probably exacerbated by the fact that most textbooks devote the most thorough explanation of MPM construction to age-structured models (where the confusing nature of postbreeding census models can be hidden by labeling an individual's age class as its age at its *next* birthday). However, when these textbooks move to a (usually much briefer) description of stage-structured models, where this solution does not work, they generally switch notation without comment (a notable exception is Mills, 2007, 2013, who calls newborns “ $N_{\text{zero}}$ ” for all models, and provides a very clear graphical depiction of both age-structured and stage-structured models).

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

How can the prevalence of these errors in MPM construction be reduced in the future? The standard recommendation from experts (including both reviewers of this paper) is that biologists should think carefully about what happens to individuals over the course of a timestep, think carefully about how the data relate to these events, and assemble everything in such a way that each transition spans a timestep. In essence, this advice boils down to “think like a modeler.” In our experience, non-modelers require a lot of interactive tutorial examples to really learn this process. Current textbooks do not provide this; the best published examples we have seen are in articles describing modeling approaches for migratory species (e.g., Fig. 28.2 of Runge and Marra, 2005). It is impossible to know how many instructors provide effective classroom teaching on this topic, but our analysis of the COMADRE database indicates that a substantial number of biologists have not adequately internalized this message.

Clearly, there is a role for improved training materials (see below). In the meantime, is there anything that biologists seeking to construct an MPM for their species can do to increase the odds of constructing it correctly? Our analyses suggest two purely mechanical approaches that might substantially reduce error rates.

First, we note that none of the prebreeding census MPMs that we examined had errors in the fertility coefficients. While we cannot assign causality to this outcome based simply on the data, prebreeding models simply do not require dealing with the troublesome reproductive transition by maturing juveniles, and it may be that the fact that newborn survival is “left over” after constructing the survival transitions encourages a closer look at the fertility coefficient. It is also important to recognize that, if one has information on age- or stage-specific birth rates and annual survival, then that information can be used to create *either* a prebreeding or a postbreeding census model (e.g., compare Figs. 1b and 1d, noticing that the same parameters occur in both). In particular, unless there is large age-dependent variation in mortality through the breeding season, it doesn't matter whether the survival is measured from the end of one breeding season to the end of the next, or from the beginning of one breeding season to the beginning of the next. The key is that the survival be measured over a full timestep (e.g., year). Furthermore, the prebreeding and postbreeding censuses are different views into the *same model*. In particular, the estimate of  $\lambda_1$  and the elasticities of  $\lambda_1$  to underlying demographic parameters will be identical between the two representations.

Thus, we recommend that, even if the ultimate goal is a postbreeding census model, the model be constructed using the prebreeding framework. This reduces the likelihood of missing a survival term in the fecundity coefficient (as the newborn survival has to be put somewhere), and eliminates the non-intuitive fertility coefficients associated with transitions into reproductive classes. If a postbreeding census

model is desired (e.g., so that model output can be compared with census data that includes newborns), then the prebreeding census model can be used to check the accuracy of the independently created postbreeding census model (e.g.,  $\lambda_1$  should be identical for the two matrices). In addition, for the simple sorts of models represented by Figs. 1 and 2 (e.g., without clonal reproduction or multiple genders), the conversion of a matrix from a prebreeding representation to a postbreeding representation is a purely mechanical process that can be automated in software. The `pre_to_post` function in the **mpmtools** R package (Kendall, 2019) provides an example of this.

Second, we found that most models in which a conceptually age-structured population had been collapsed into a small number of stages, each with a well-defined mean stage duration, were constructed in ways that would fail to reproduce the asymptotic growth rate—indeed, in our case studies this error had the largest impact on  $\lambda_1$  estimates. We interpret this as being because the best stage-based approximation—the AAS model—is both conceptually and computationally challenging to produce. For simple life histories, we recommend using the **mpmtools** R package (Kendall, 2019) to automatically construct an AAS model from information on stage-specific demography and duration. More generally, if the among-individual stage variation is not too great (i.e., all individuals mature at about the same age), then we recommend that the stage be “unrolled” into a Leslie matrix model. This creates a model that makes correct projections under both transient and asymptotic conditions, and can be used both for projecting the population and for calculating life history statistics. This also allows the demographic rates to vary with age within a stage (e.g., for species such as fish with size-dependent demography), avoiding further pitfalls highlighted by Fujiwara and Diaz-Lopez (2017). We recognize that in long-lived species the results of sensitivity and elasticity analyses are often more useful when aggregated by stage (Fujiwara and Diaz-Lopez, 2017); we recommend performing this aggregation *after* analyzing the age-structured model (e.g., by summing the elasticities associated with all the age classes within a stage).

Another reason for preferring age-structured to stage-structured models (when appropriate) is for the accurate calculation of generation time. Stage structured models in general are not particularly suitable for estimating generation time (Fujiwara and Diaz-Lopez, 2017; Lebreton, 2005). This is because stage structured models lump individuals in multiple age classes into a single stage treating them equally. This is a reasonable simplification if we are only calculating asymptotic population growth rate and stable stage distribution. However, all individuals, regardless of duration of time spent in a stage, are treated equally to have the same rate of transitioning to another stage. This has a large effect on generation time estimation. Therefore, it is strongly recommended that generation time calculation should be based on an age structured model unless stage transitions are truly age-independent.

When the stage durations are not fixed, a more advanced solution is to develop a model that incorporates both age and stage (Caswell et al., 2018; Lebreton, 2005). In this case, an accurate characterization of the distribution of stage durations can be critical for many analytic outcomes, as described by de Valpine et al. (2014) for continuous-time models. However, estimating the parameters of such distributions can be challenging (see, e.g., the derivation of parameters for time to next breeding in sea turtles by Ebert, 1998).

Experts can also help, by developing handbooks and training materials that are both comprehensive and clear to non-modelers, who are experts in biology and ecology but novices at modeling. The comprehensiveness requires, in part, a thorough treatment of stage-structured models (which are not described as completely as age-structured models in many texts), as well as a comprehensive discussion of the consequences of various choices of when the census should occur in the model. The clarity certainly requires consistent notation and terminology, as well as attention to the knowledge level of the audience, but that will probably not be sufficient. Educational research suggests that

when students arrive with misconceptions, clear and accessible expositions of correct principles do not lead to learning, as the students do not pay sufficient attention to recognize the difference between the exposition and their prior belief; better learning occurs when they are first presented with the misconception and then led to an understanding of why it is wrong (Muller et al., 2008a,b). The biologically-based intuitions that underlay incorrect formulations of MPMs may have the strength of scientific misconceptions, in which case the training material will need to actively uproot them before a better understanding of the model requirements can be learned.

One pedagogical approach that may be helpful is to build “seasonal” sub-models, and use matrix multiplication to generate the integration over the full timestep (rather than requiring the integration to be done in the brain of the model builder). Williams et al. (2002) do this (for age-structured models only; section 8.4.2), creating “survivorship” and “reproduction” matrices and showing how they can be combined to produce both prebreeding and postbreeding census models. Periodic matrix models are generally presented as advanced topics (the notation in Caswell’s 2001 treatment of the topic is intimidating to non-modelers), and are typically applied to either annual species or species that breed continuously (at seasonally varying rates) throughout the year. Nevertheless, a more accessible presentation of periodic matrix models, showing how they can be used to integrate demographic processes that happen at different points in the annual cycle, might help alleviate many of the problems identified here. Such an approach to MPM construction might also encourage the development of models that more fully incorporate the richness of within-year life history processes.

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

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

While our analysis has focused on animal MPMs, we note that plant MPMs may be subject to similar errors as those described here. In addition, the construction of size-structured MPMs faces challenges that are qualitatively similar to those for stage-structured MPMs, while differing in detail; and ambiguities around the treatment of seeds and seed banks create the potential for additional errors in the fertility coefficient. Thus, a systematic analysis of published plant MPMs may be warranted.

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,  $\lambda_1$ ) and qualitative (e.g., mis-ranking the elasticity of  $\lambda_1$  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. While some analysis endpoints seem to be broadly robust to matrix construction errors (especially errors in the fertility coefficient), there may be some cases in which the scientific conclusions or management recommendations supported by those models could 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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## Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolmodel.2019.03.011>.

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