

1 Persistent problems in the construction of matrix
2 population models

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8 **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 as well as fertility in the reproduction term; (2) introducing a one-year delay in age at first reproduction; and (3) incorrectly calculating the growth transition rate out of a stage with a mean development time greater than the model time step. We review the sources of such errors and provide new analyses revealing the impact of such errors on model predictions. These MPM construction issues are treated extensively in textbooks, so their existence in current literature is surprising. 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 41% and 42%, respectively, of the published studies; all were in models that used a "post-breeding census" representation of the life cycle graph (in which newborns [eggs, neonates, fledglings, etc.] are explicitly included). Of the studies where stages may last longer than one time step, 25% constructed the growth rate using inappropriate formulas, and 37% used methods that were either undescribed or would generate the correct development time only if the population remained at the observed within-stage age structure. 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 undertaken with caution.

9 *Key words:* COMADRE animal matrix database, Lefkovitch matrix, Leslie
10 matrix, Matrix population models

11 1. Introduction

12 The use of matrix population models (MPMs) for the ecological study of
13 plants and animals has expanded rapidly in recent years (Salguero-Gómez
14 et al., 2016, 2015). MPMs are a convenient way to synthesize demographic
15 information about a population, and are useful in addressing ecological,
16 evolutionary, and management questions (Caswell, 2001; Morris and Doak,
17 2002). Most early MPMs were developed by collaborations between biologists
18 with expertise on the species at hand and modelers with deep understanding
19 of the subtleties of modeling. MPMs now, having been long promoted as
20 a straightforward translation of life-history information into quantitative
21 analysis, are often being created by biologists who are primarily empirical
22 ecologists or conservation biologists, and may have had little training in
23 modeling beyond a graduate course in population ecology. One might then
24 ask, do these MPMs reliably reproduce the life histories they are meant to
25 represent?

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

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38 If it does not, then we are introducing additional errors into the analysis
39 above and beyond the inherent approximations of modeling.

40 One of us (BEK) has spent two decades teaching MPMs to applied
41 masters students. This experience has revealed several aspects of MPM
42 construction that are particularly challenging to novices, and thus might be
43 similarly challenging to biologists who do not regularly create mathematical
44 models of their system. Furthermore, the students, when sent to find a
45 published model to analyze, have uncovered a suprising number of published
46 MPMs that have failed to meet these challenges. At one level, the errors
47 made by these novices are “simply” accounting issues, but our interpretation
48 is that the difficulty that students have in overcoming them is rooted in
49 the contrast between the often-loose way that terms are used to describe
50 biological populations and the very precise meanings of terms in MPMs
51 (together with some genuine linguistic ambiguity that plagues the field).

52 Our goal in this paper is to highlight these challenges (which are described
53 in the next section), quantify their impacts on the outputs of MPMs, and
54 document their prevalence in the peer-reviewed literature. We conclude with
55 a discussion of why these MPM construction errors are so prevalent, and
56 how we might improve future practice

57 2. Challenges in MPM construction

58 Matrix population models operate in discrete time, and as such are
59 most naturally suited to species whose reproduction is concentrated in a
60 short breeding season (so-called “birth-pulse” populations; Caswell, 2001
61 *[did Caswell coin this phrase?]*). Many animals and plants satisfy this
62 assumption, and we will focus on this case in our analysis. However, much of
63 the theoretical development of MPMs was motivated by human demography,
64 in which reproduction occurs throughout the year (“birth-flow” populations).
65 This ~~requires~~ a variety of mathematical approximations to suitably transform
66 continuous-time processes into a discrete-time representation, and gives a
67 **different** view of the identity of individuals in a particular age or stage class.
68 We will not treat the former here, but the latter is relevant.

69 MPMs assume that the population at time t is a snapshot at a particular
70 “census date.” The discretization of age into classes means that in a birth-flow
71 population, the first age class represents all individuals between zero and
72 one timestep old at time t , and thus we would describe it as “Age 0–1.”
73 In contrast, in a birth-pulse population, all individuals in an age class are
74 (more-or-less) exactly the same age. If the census were taken immediately

75 after the breeding season¹ (a “post-breeding census”), the first age class
76 would comprise newborn individuals, all of age zero, the second class would
77 comprise individuals of age exactly one, etc.² In contrast, if the census were
78 taken immediately before the breeding season (a “pre-breeding census”), the
79 youngest age class would be made up of individuals all with age exactly one.
80 But we often see birth-pulse models in which the age classes are given as a
81 range—this is incorrect, and leads to ambiguity (does the class “Age 0–1”
82 refer to newborns or to one-year-olds?) that can confuse the practitioner
83 on how best to construct the model. This nomenclature problem likely
84 has two sources. First, many texts introduce birth-flow models first (e.g.,
85 the very first figure in Caswell, 2001, illustrating the notion of discrete age
86 classes, shows the classes as ages 0–1, 1–2, etc.). Second, in colloquial use,
87 age-associated terms often span an age range: for example, in ungulates the
88 term “yearling” refers to any individual between the ages of one and two.
89 When that same term is applied to a class in a birth-pulse MPM, nontrivial
90 cognitive effort is required to mentally redefine it (so that “Yearling” means
91 age exactly one).

92 This nomenclatural ambiguity plays a role in all three of the “accounting
93 errors” that follow. An additional challenge is that most textbooks use incon-
94 sistent notation and subscripting conventions for age- and stage-structured
95 models. Age-structured models follow a convention that makes sense for a
96 continuously breeding species: an individual is assigned to an age class that
97 is numbered with the individual’s age at its *next* birthday (but note that this
98 differs from colloquial use in most languages, where we identify a person’s
99 age with their *previous* birthday). When looking at a species with discrete
100 breeding seasons, this convention is perfectly fine for a pre-breeding census
101 model, as all individuals are just a tiny fraction of a timestep away from
102 their next birthday, and an individual that is almost three years old will
103 have characteristics almost indistinguishable from one that is exactly three
104 years old. In contrast, for a post-breeding census model, this convention
105 would identify an individual that is just a tiny bit past its third birthday as
106 a four-year-old. This means that “ x -year-old survival” (often denoted P_x)
107 refers to survival from age x to age $x + 1$ in a pre-breeding census model,

¹Defined as the season in which individuals are born, not the season during which their parents mate.

²In principle, the census could occur at any time relative to the breeding season, and Caswell (2001) provides general formulas to account for this; but in practice the two cases described here encompass nearly all, if not all, published birth-pulse models.

but from age $x - 1$ to age x in a post-breeding census model.

This is potentially confusing, but most practitioners don't move between these models so it is probably not a large issue. However, transitioning from an age-structured model (which is what all textbooks use for a detailed explanation of MPMs) to a stage-structured model creates huge problems, at least for post-breeding census models. This is because, whereas an individual that was x years old at its recent birthday will be exactly $x + 1$ years old at its next birthday, and can be unambiguously identified as "age class $x + 1$," an individual that was in stage x at its recent birthday might be in any of a number of stages at its next birthday, preventing the application of the age-structure convention. The solution is for post-breeding census stage-structured models to assign individuals to the stage class they were in at their recent birthday. This is perfectly sensible, but *most textbooks make this transition without comment*. [CHECK WHAT MILLS DOES HERE] Thus it is not obvious to a novice that the carefully-explained conventions of age-structured models no longer apply; we suspect that this contributes to some of the common errors described below.

To avoid the need to be pedantic when moving between age- and stage-structured models, we will apply the stage-structured convention to age-structured models. Thus, in a post-breeding census, individuals that have just been born are classified as "age zero" or "newborn," with a subscript of zero. This will make our exposition clearer, but it is important to note that our lifetables and age-structured models will therefore look different from most textbooks.



2.1. Ensuring that the fertility transition spans a full timestep

In a life table (e.g., Table 1, age specific survival and birth rates look functionally equivalent. But there is an important difference: survival (often denoted P_x (most common, but has a different meaning in stage-structured models), s_x , or σ_x , where x is the age or stage; we will use σ_x) represents the fraction of individuals in class x that survive for a full timestep, from time t to time $t + 1$. In contrast, the birth rate (typically denoted b_x or m_x ; we use the former) is instantaneous: it is the number of offspring produced at time t by an individual that is alive at time t . It is tempting to draw a life-cycle diagram like the one in Fig. 1a (and we commonly see that 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 transition in the matrix must span a timestep, and m_x does not accomplish that.

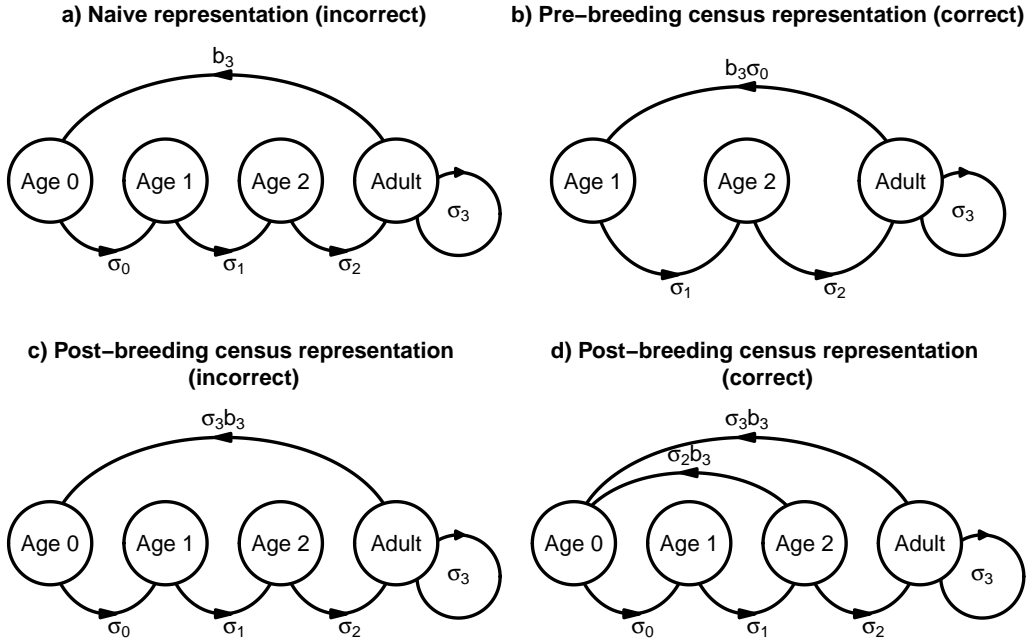


Figure 1: Four life-cycle diagrams that might (or might not) represent the life table in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the reproductive transitions must span a timestep and therefor include a survival term. (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) A post-breeding census representation, in which the adult burth 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.

Table 1: A sample life table for a species that reaches sexual maturity at age 3 (adult stage). Adults continue to survive and reproduce indefinitely 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

146 To get the timestep in there, we need to multiply b_x by somebody's
 147 survival—either the parent or the offspring. For a pre-breeding census
 148 model, the reproductive transition is $F_x = b_x \sigma_0$: the parent, in class x ,
 149 produces b_x offspring immediately after the census, and then these offspring
 150 survive to the end of the timestep at rate σ_0 (Fig. 1b). For an annual
 151 timestep, the transition F_x represents the number of one-year-olds next year
 152 produced by an individual in class x this year.

153 In a post-breeding census, the parent (which will have just reproduced
 154 if it is already an adult) must survive for a timestep, aging by a timestep
 155 and possibly maturing into a new class, and then reproduces with a birth
 156 rate appropriate to its class at the end of the timestep. If we use x' to
 157 denote the parent's class at time $t + 1$, then the transition is $F_x = \sigma_x b_{x'}$ (Fig.
 158 1d). For an annual timestep, F_x is the number of zero-year-olds (newborns)
 159 next year produced next year by an individual that was in class x this year.
 160 Properly accounting for x' is a separate challenge that we address in the
 161 next subsection.

162 2.2. Matching the age at first reproduction to the species' life history

163 In an age-structured population, the lowest age with a non-zero birth
 164 rate represents the **age at first reproduction**; let us call that x_m , for “age at
 165 [reproductive] maturity.” In a post-breeding census model, the individuals
 166 who are age x_m at the end of the timestep, and have just reproduced for the
 167 first time, were age $x_m - 1$ at the beginning of the timestep. This creates a
 168 reproductive transition from age class $x_m - 1$ to age class zero—the lower

169 of the two reproductive transitions in Fig. 1d. Embracing this transition
 170 requires overcoming cognitive dissonance—“juveniles” are reproducing!—
 171 and failure to do so results in models like that in Fig. 1c. Pre-breeding
 172 census models do not cause this problem; as the newly matured, about-
 173 to-reproduce-for-the-first-time individuals are already classified as age x_m ,
 174 matching intuition.

175 This is also not a challenge for post-breeding census models if we follow
 176 the convention of associating the age class with the age at the individual’s
 177 next birthday. Then the reproduction by newly maturing individuals is
 178 $F_{x_m} = P_{x_m} b_{x_m}$ (we use P for survival to clarify that it is a differently indexed
 179 parameter from σ as used above); the cognitive dissonance is finessed by
 180 “hiding” the fact that these individuals started the timestep as juveniles.
 181 Indeed, this is a strong justification for the convention. However, this
 182 convention cannot be maintained when moving from age-structured to stage-
 183 structured models; since most animal MPMs are at least partially stage
 184 structured, we suspect that textbooks’ failure to force a confrontation with
 185 this cognitive dissonance in the conceptually simpler age-structured models
 186 leaves practitioners unprepared to face it (or even recognize its necessity) in
 187 stage-structured models.

188 The simplest stage-structured model has newborns, a nonreproductive
 189 juvenile class that spans multiple timesteps, and reproductive adults (Fig.
 190 2). Within the juvenile class, some individuals remain juveniles in the next
 191 timestep (should they survive), whereas others mature into adults. If γ_j is
 192 the fraction surviving individuals that mature (“grow”) at the end of the
 193 timestep, then the Juvenile–Juvenile transition is given by $P_j = \sigma_j(1 - \gamma_j)$
 194 and the Juvenile–Adult transition is given by $G_j = \sigma_j\gamma_j$. This is true for
 195 both pre-breeding and post-breeding census models. However, for the latter,
 196 the individuals that made the Juvenile–Adult transition were already adults
 197 at the just-passed breeding season, and hence have had their first opportunity
 198 to reproduce. Thus we need a reproductive transition leading out of the
 199 juvenile class— $F_j = G_j b_a$ —which again seems to defy common sense. There
 200 is no way to finesse this in the way that has been done in age-structured
 201 models: if we classify individuals by their stage at their next birthday, so that
 202 the maturing individuals are called “adults,” then we impose a constraint
 203 that individuals in the last year of the juvenile stage have the same survival
 204 as adults, which often isn’t accurate. There are further obstacles to any
 205 attempted finesse in more complicated models in which individuals can
 206 “mature” into more than one subsequent class.

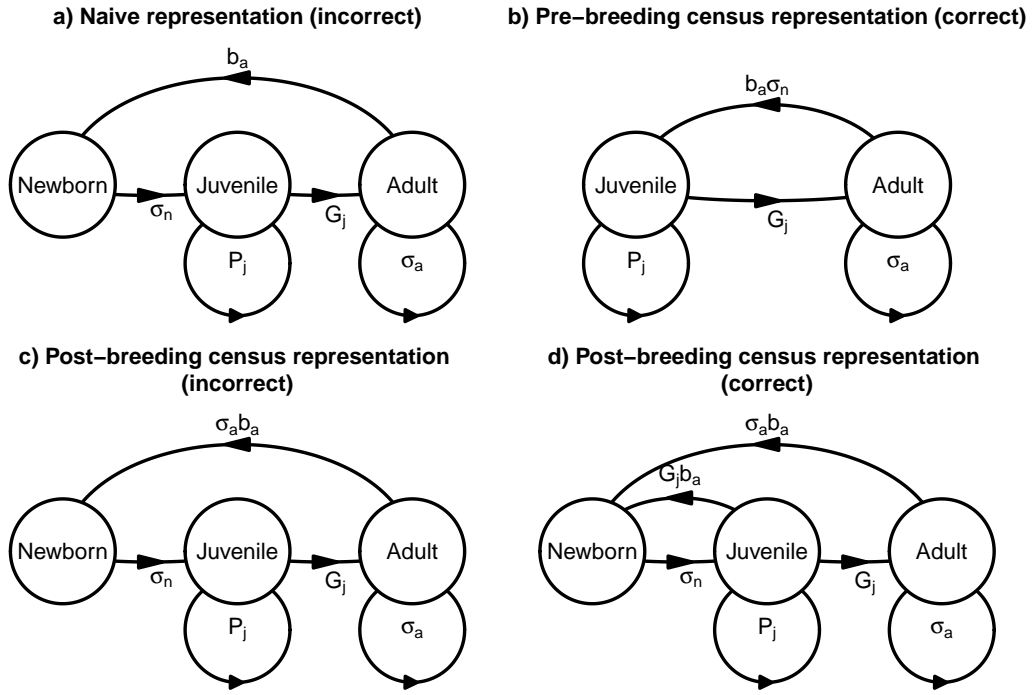


Figure 2: Four life-cycle diagrams that might (or might not) represent stage structured life table in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the reproductive transitions must span a timestep and therefore include a survival 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) A post-breeding census representation, in which the adult burth 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.

In both stage- and age-structured models, failing to have the reproductive transition out of the last juvenile class in post-breeding census models will lead to a one-year delay in the age at first breeding, relative to the life history that the model is meant to represent.

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 maturing out of stage x . With longitudinal data on individuals, one can simply derive this from the observations, for example using multistate CMR models (CITE, although this is not guaranteed to be robust; see Discussion). However, 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), then the goal is to create a “stage-for-age” model (e.g., Ebert) where the mean stage duration in the model equals the fixed stage duration in the life history. Even where real stage durations are somewhat variable, if there is a well-defined mean stage duration, then we can still aspire to have the modeled mean stage duration match the actual mean stage distribution.

Caswell (2001) has a section of his book describing various ways of doing this. It's not clear that there is a single “best” approach, as the stage-structured model will never match the age-structured model in all ways (see Discussion). Nevertheless, the primary analyses performed on most published MPMs are to calculate the asymptotic growth rate (λ) and the sensitivity of λ to underlying demographic parameters. For these calculations, there is one (and only one) recipe to create a stage structured model that will generate the same results as the equivalent age-structured model with fixed stage durations. 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); it is covered in Caswell's (2001) section on stage-structured models.

The basic idea is that γ represents the fraction of individuals in the stage that have spent enough time in the stage to mature. This, in turn, depends on the (virtual) age structure within the stage. In general, this age structure could have any form, depending on the recent history of the population; the one time it is well defined is when the population is at the stable age/stage distribution. This is exactly the condition for calculating λ .

Under these conditions, 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 survival, which determines how a cohort shrinks as it ages. The second is the population growth rate, which determines the degree to which one year's entering cohort is larger or smaller than the previous one. This makes γ non-trivial to calculate, as the resulting formula involves λ , which can only be calculated once the MPM has been constructed! The solution is an iterative approach: take an initial guess of λ , calculate γ from the formula; calculate the dominant eigenvalue of the resulting matrix; use that as a new guess for λ ; and repeat until the value of λ stops changing. For someone used to programming, this is straightforward to implement; but non-modellers find this daunting, and we do not know of any programs that implement this algorithm, aside from some difficult-to-generalize Matlab code in Morris and Doak (2002). **Check this out**

Thus, non-modellers will be tempted by easier-to-calculate formulas. Some discover a predecessor to the above formula (Crouse et al., 1987) that had been developed for the same population studied by Crowder et al. (1994). This formula is complex-looking but straightforward to calculate, as it doesn't require iteration (it incorporates the within-cohort dynamics, but *assumes* that $\lambda = 1$). An even simpler approach is to simply say that, if the stage duration is T timesteps, then the fraction maturing is $1/T$. This effectively assumes that the age distribution is perfectly flat. Its popularity probably stems not just from the fact that it is simple to calculate and explain, but because it is the first solution to the problem listed by Caswell (2001), who seems to endorse it. **Check Caswell's actual wording**

We will refer to these as the "asymptotic age structure" (AAS) model, the "stationary age structure" (SAS) model (where "stationary" means that the population is neither growing nor declining), and the "flat age structure" (FAS) model. As mentioned above, only the AAS model will replicate λ and its sensitivities from the fully age-structured model.

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), sensitivity analysis of λ 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)

282 and by examining two case studies: a lionfish (*Pterois* sp.) model with very
 283 high population growth (Morris et al., 2011), and a pair of American alligator
 284 (*Alligator mississippiensis*) models that project rapidly declining and nearly
 285 constant population dynamics, respectively (Dunham et al., 2014). These
 286 studies made all three of the errors described above; we singled them out
 287 not because they are particularly egregious (many other studies make these
 288 errors) but because ~~they do~~ an exceptional job of describing the species' life
 289 history, allowing us to infer the model they meant to construct. All three of
 290 these models had other minor errors, which we corrected (while retaining the
 291 three focal errors) to create "baseline" models. We then constructed models
 292 that fixed one, two, or three of the focal errors to see how these errors affect
 293 the model projections and conclusions.

294 A matrix population model for lionfish was constructed by Morris et al.
 295 (2011) to investigate the potential approaches for controlling the invasive
 296 species. The ~~model consist~~ of three stages (larvae, juvenile, and adult),
 297 and time step of the model is one month. The original model was a post-
 298 breeding census model, but it did not include the survival of adults in the
 299 fertility rate. The average duration of the juvenile stage was assumed to
 300 be 12 months in the model. This meant they take 14 months for the first
 301 reproduction (one month in larvae stage, 12 months in juvenile stage, and
 302 one additional month in fertility rate) even though they start reproducing
 303 in 12 months. The authors used FAS model for calculating the transition
 304 rates for juveniles. We developed four stage-structured population models
 305 that gradually correct for some or all of these problems and one Leslie
 306 matrix (Table 2). Along with the original models, we used the six models
 307 to calculate λ , stable stage distribution, reproductive value, sensitivity and
 308 elasticity of λ to stage-specific survival rate and fecundity, damping ratio,
 309 and generation time (Appendix 1).

310 For American alligator populations, Dunham et al. 2014 developed two
 311 stage-structured matrix population models to compare the status of northern
 312 and southern populations. The original models consist of five stages (eggs,
 313 larvae, juvenile, subadults, and adults), and the time step of the model is one
 314 year. Similarly to the lionfish model, the alligator models are post-breeding
 315 census models, but the authors did not include the survival of adults in
 316 the fertility rate. The first stage was egg stage, but it only lasted for three
 317 months; therefore, there was clear inconsistency in the time steps among
 318 stages. Dunham et al. used AAS model to calculate transition rates for
 319 juvenile and subadult stages. We developed two additional stage-structured

models that corrects some or all of these problems and one Leslie matrix for each population (Table 1). The four population models for each population were used to calculate the same quantities that we calculated with the lionfish models (Appendix 1).

Table 2: List of models and description of changes made to the original models.

Population	Model Description	
Lionfish	L1	- Original three-stage model in Morris et al., 2011
	L2	- Correction of juvenile duration - Incorporation of adult survival in fertility rate
	L3	- All of the corrections in L2 - Incorporation of fertility rate of juvenile stage
	L4	- All of the corrections in L3 - Use of SAS model for calculating juvenile transition rate
	L5	- All of the corrections in L3 - Use of AAS model for calculating juvenile transition rate
	L6	- Leslie matrix
American Alligator (Northern)	A1	- Original five-stage model in Dunham et al. 2014
	A2	- Reduction in the number of stage to four (hatchling, juvenile, subadult, and adult) - Incorporation of survival rate into fertility rate of adult stage - Addition of fertility rate to subadult stage
	A3	- All of the corrections made in A2 - Calculation of juvenile transition rates using AAS model
	A4	- Leslie matrix
American Alligator (Southern)	A5	- Original five-stage model in Dunham et al. 2014
	A6	- Reduction in the number of stage to four (hatchling, juvenile, subadult, and adult)

Population	Model Description
	- Incorporation of survival rate into fertility rate of adult stage
	- Addition of fertility rate to subadult stage
A7	- All of the corrections made in A6
	- Calculation of juvenile transition rates using AAS model
A8	- Leslie matrix

3.1. Effects on asymptotic population growth rate (λ)

The original lionfish model (L1) had λ of 1.125; this meant they grew by 12.5% each month (Figure S1). Even though they are invasive species and rapidly expanding. The population growth rate is unrealistically high. By reducing the average duration in juvenile stage (L2) and incorporating fertility rate on juvenile stage, the population growth rate increased further (L3). However, the use of SAS model to calculate the juvenile transition rate (L4) reduced λ substantially. This is because for the duration of the juvenile stage (11 time steps on average), the survival rate is low. Incorporation of λ in calculation of the transition rates (AAS models; L5) reduced λ because $\lambda \gg 1$. This meant that there was an increase in number of individuals recruited into juvenile stage from larval stage; therefore, the actual age-distribution declines faster with age than the stable age distribution. The Leslie matrix (L6, which is expected to be least prone to the errors associated with the manipulations of parameters, and model L5 had the same λ .

The original alligator models had λ of 0.87 for the northern population and 1.02 for the northern population (Figure S8). In contrast to lionfish example, λ was affected very little with the corrections. Changes in the fertility rate had very little effect because λ was not sensitive to fertility rate. Changes in the transition rates for juvenile and subadult stages had little effect because, for the short durations in the stages (7 years in each stage and 3 years in each stage for northern and southern populations, respectively), they had relatively high survival rates (0.78 and 0.73 for juvenile and subadult stages of both populations).

3.2. Effects on sensitivity analysis of λ

Similarly to the results on λ , sensitivity and elasticity of λ to stage-specific survival and fecundity were affected more for lionfish than alligator. 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 (Figures S4 & S5). This implies that conservation strategy can be affected by the errors in developing a population matrix.

For lionfish models, changes in sensitivity and elasticity are less clear (Figures S11 & S12), but stable stage distribution (Figure S9) and reproductive values (Figure S10) are affected by the errors. These quantities are used for calculating sensitivity and elasticity of λ . For example, the original model substantially under-estimated the stable stage distribution and over-estimated the reproductive value of adults.

3.3. *Effects on life history statistics*

Damping ratio is a measure of how long transient dynamics lasts in a system after a perturbation, and generation time is a measure of time scale of populations. These quantities are expected to be affected by converting the age-structured into stage-structured models.

4. Prevalence of construction errors in published MPMs

4.1. *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.

Using a haphazard subset of studies, we developed a protocol to systematically assess each study (Appendix 2). This protocol was applied by NNN members of the COMADRE digitization team (“Compadrinos”), all graduate students in demography at the Max Planck Institute for Demographic Research. After initial training, consistency was ensured by having all members of the team, 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

387 answer was coded “NA;” if the answer could not be determined from the
 388 information in the publication, it was coded as “unknown.”
 389 Questions related to fertility
 390 Questions related to first reproduction
 391 Questions related to maturation
 392 Statistical analysis: means, trends through time

393 4.2. Results

394 *Note: The data collection by the Compadrinos is ongoing. Here we report*
 395 *an analysis based on data collected for the initial feasibility study for the*
 396 *project. The publications are recent and haphazardly chosen, but for this*
 397 *preliminary review we have analyzed and presented these data in the same*
 398 *form that we plan for the final dataset.*

399 We were able to unambiguously identify the components of the fecundity
 400 term in 24 studies. 50% of these studies failed to include an appropriate
 401 survival component in the reproduction terms; 100% of these errors were in
 402 post-breeding census models. The frequency of these errors had no detectable
 403 trend over time ($P = 0.539$; Fig. 3a).

404 The potential for missing the reproductive event associated with first
 405 reaching reproductive age is only a feature of post-breeding census models.
 406 Of the 18 studies in which we could unambiguously determine both the
 407 last pre-reproductive stage or age class and in which we could identify
 408 reproductive transitions, 67% made this error. The frequency of these errors
 409 had no detectable trend over time ($P = 0.495$; Fig. 3b).

410 16 studies included models having at least one stage class that was meant
 411 to last for multiple timesteps; we were able to unambiguously classify the
 412 rule defining the maturation rate out of the stage(s) in 11 of them. Of these,
 413 55% did not use a rule that would generate a value of λ that would match
 414 an age-structured model with the target mean stage duration (Fig. 4). The
 415 frequency of these errors had no detectable trend over time ($P = 0.842$; Fig.
 416 3c).

417 5. Discussion

418 *[This outline will be fleshed out in the final version!]*

- 419 A. Summary of impacts
- 420 B. Summary of prevalence

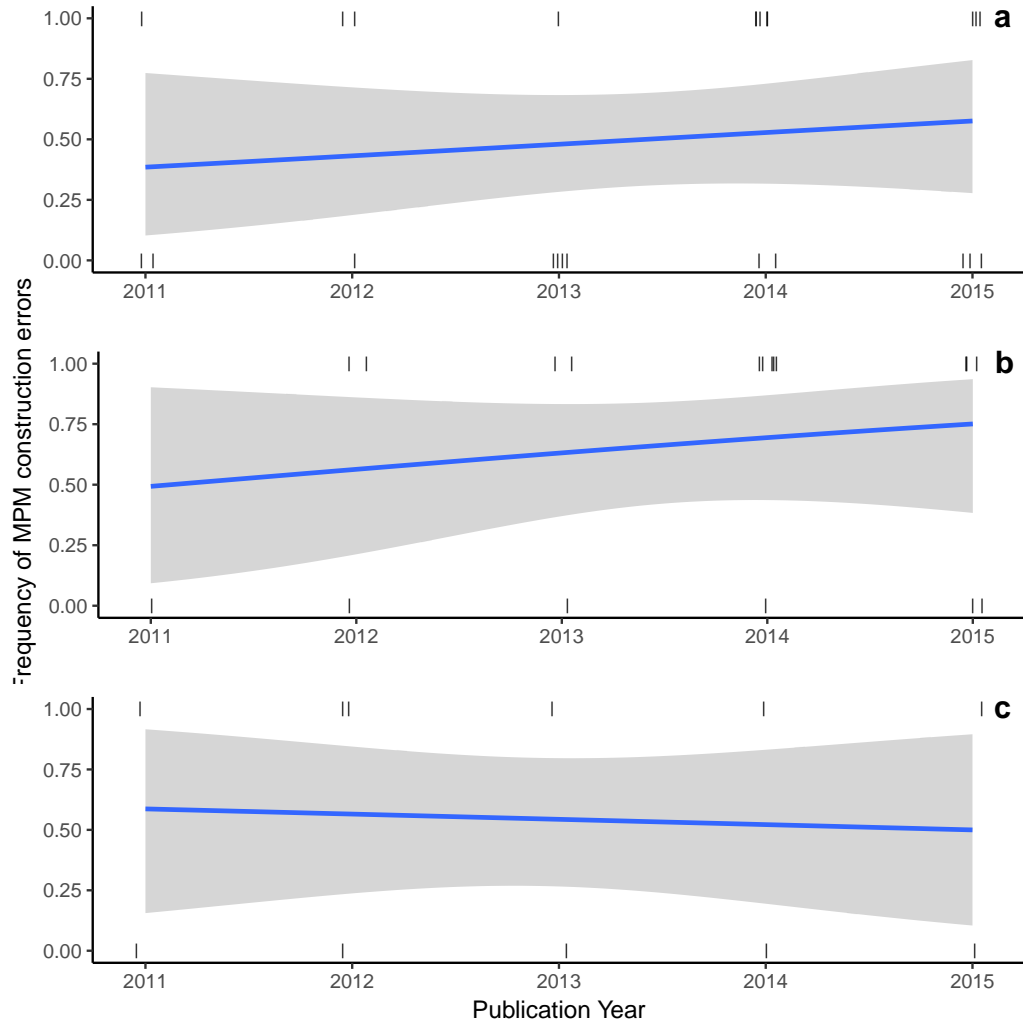


Figure 3: Trends in matrix population model construction errors through time. Trend line is logistic regression; vertical lines represent the data (jittered horizontally to prevent overlap). (a) Frequency of errors in reproduction term, among all studies. (b) Frequency of errors in timing of first reproduction, among studies with post-breeding census models. (c) Frequency of errors in mean stage duration, among studies with stage classes having mean stage durations > 1 timestep.

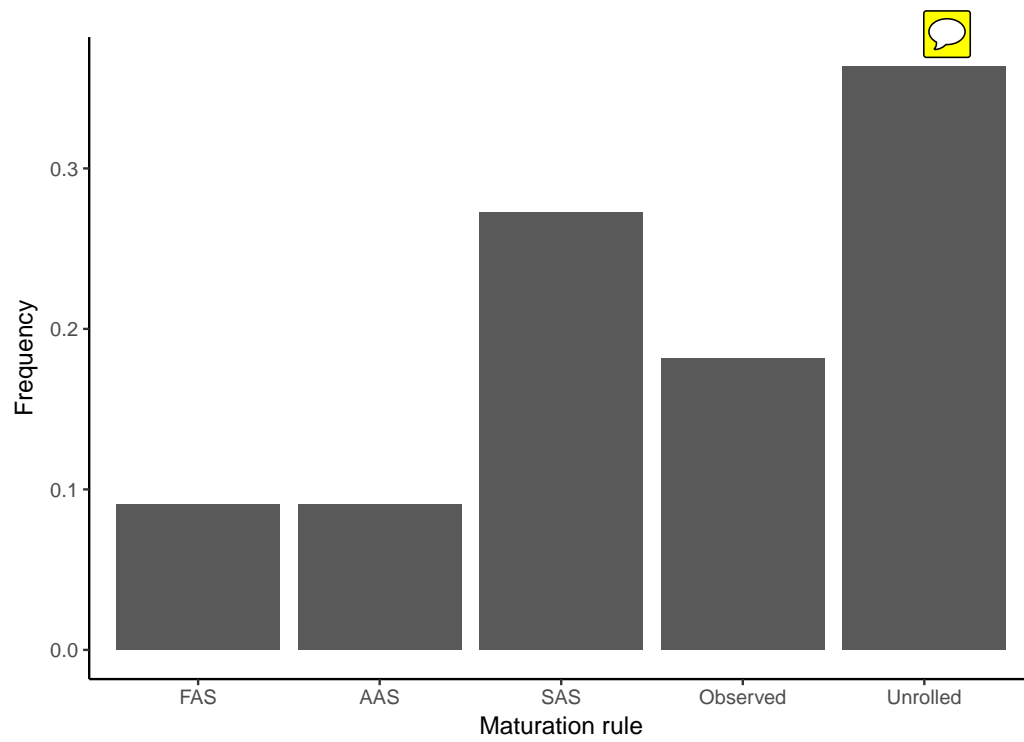


Figure 4: Frequency of approaches for setting maturation rates from stages with mean duration exceeding one timestep.

- 421 C. Why does this happen? Most texts are incomplete (especially for
422 stage-structured models) and/or have inconsistent or confusing notation.
423 Talk about Caswell (2001) as example. Also, these are “threshold
424 concepts.”
- 425 D. Recommendations for practitioners:
- 426 1. Use prebreeding census whenever possible
 - 427 2. Unroll developmental stages (address sensitivity analysis chal-
428 lenges raised by Fujiwara and Diaz-Lopez, p. 2: “The inclusion
429 of a large number of age-classes for long-lived organisms can
430 make the interpretation of the sensitivity and elasticity analy-
431 ses complicated because individuals in multiple age classes are
432 often practically identical but separated in an age-structured
433 model. Consequently, when long-lived organisms are studied, it
434 is common to convert age-specific vital rates into stage-specific
435 vital rates, and to use stage-structured population matrices for
436 calculating λ and generation time.”)
- 437 E. Recommendations for experts:
- 438 1. Develop handbooks and training materials that are both compre-
439 hensive and clear to novices (reference threshold concepts)
 - 440 2. Develop software tools to help guide practitioners through the
441 process of translating demographic information in to MPMs
- 442 F. Revisiting prior results
- 443 1. Individual studies
 - 444 2. Syntheses

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449 evaluation protocol, and [list of compadritos who actually worked on the
450 project] for carrying out the model evaluations.

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453 and interpretation, 2nd ed. Sinauer Associates, Sunderland, MA.
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