

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 season<sup>1</sup> (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.<sup>2</sup> 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,

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

<sup>2</sup>In 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.

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

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

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

### 132 2.1. Ensuring that the fertility transition spans a full timestep

133 In a life table (e.g., Table 1, age specific survival and birth rates look  
134 functionally equivalent. But there is an important difference: survival (often  
135 denoted  $P_x$  (most common, but has a different meaning in stage-structured  
136 models),  $s_x$ , or  $\sigma_x$ , where  $x$  is the age or stage; we will use  $\sigma_x$ ) represents the  
137 fraction of individuals in class  $x$  that survive for a full timestep, from time  $t$   
138 to time  $t + 1$ . In contrast, the birth rate (typically denoted  $b_x$  or  $m_x$ ; we  
139 use the former) is instantaneous: it is the number of offspring produced  
140 at time  $t$  by an individual that is alive at time  $t$ . It is tempting to draw a  
141 life-cycle diagram like the one in Fig. 1a (and we commonly see that in the  
142 literature). While this works as a *conceptual* diagram, translating it directly  
143 into an MPM by coverting each arrow in the graph into a matrix element is  
144 incorrect: each transition in the matrix must span a timestep, and  $m_x$  does  
145 not accomplish that.

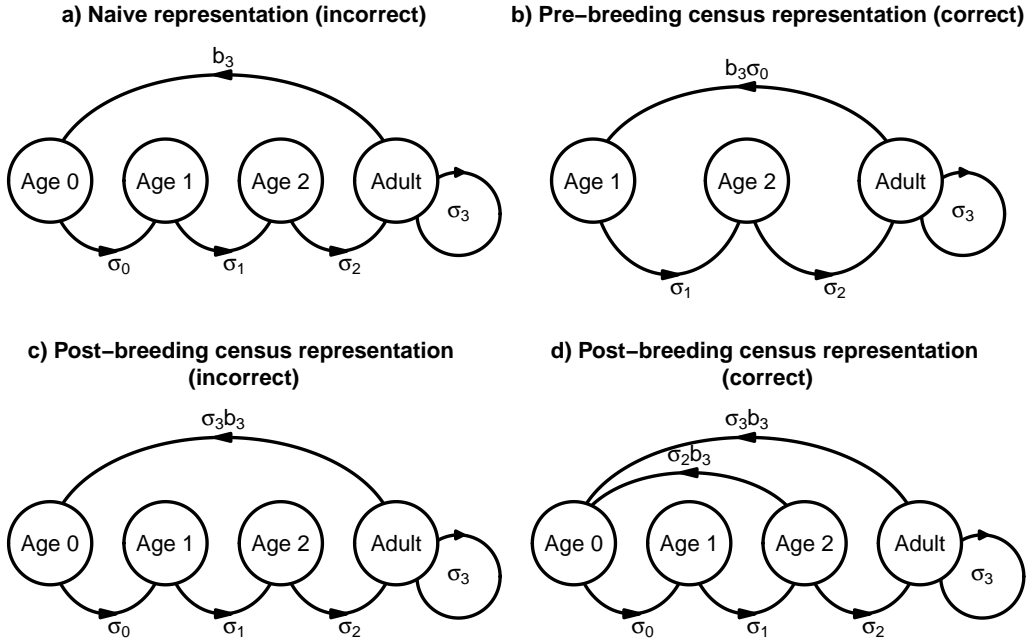


Figure 1: Four life-cycle diagrams that might (or might not) represent the life table in Table 1. (a) A “naive” representation that associates each arrow with a vital rate. This fails to account for the fact that the reproductive transitions must span a timestep and therefor include a survival term.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

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  $\sigma_0$  (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 transision 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  $\sigma$  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). **Make SS lifecycle graphs** Within the juvenile class, some individuals  
 191 remain juveniles in the next timestep (should they survive), whereas others  
 192 mature into adults. If  $\gamma_j$  is the fraction surviving individuals that mature  
 193 (“grow”) at the end of the timestep, then the Juvenile–Juvenile transition  
 194 is given by  $P_j = \sigma_j(1 - \gamma_j)$  and the Juvenile–Adult transition is given by  
 195  $G_j = \sigma_j\gamma_j$ . This is true for both pre-breeding and post-breeding census  
 196 models. However, for the latter, the individuals that made the Juvenile–  
 197 Adult transition were already adults at the just-passed breeding season,  
 198 and hence have had their first opportunity to reproduce. Thus we need a  
 199 reproductive transition leading out of the juvenile class— $F_j = G_j b_a$ —which  
 200 again seems to defy common sense. There is no way to finesse this in the way  
 201 that has been done in age-structured models: if we classify individuals by  
 202 their stage at their next birthday, so that the maturing individuals are called  
 203 “adults,” then we impose a constraint that individuals in the last year of the  
 204 juvenile stage have the same survival as adults, which often isn’t accurate.  
 205 There are further obstacles to any attempted finesse in more complicated  
 206 models in which individuals can “mature” into more than one subsequent



207 class.

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

### 212 2.3. Ensuring that the mean time in each developmental stage matches the 213 species' life history

214 The final challenge is associated with estimating  $\gamma_x$ , the fraction of  
215 individuals maturing out of stage  $x$ . With longitudinal data on individuals,  
216 one can simply derive this from the observations, for example using multistate  
217 CMR models (CITE, although this is not guaranteed to be robust; see  
218 Discussion). However, in many cases, the goal is to combine information on  
219 stage-specific survival, often variously collected, with knowledge about the  
220 stage duration (the number of timesteps that individuals remain in a stage  
221 before maturing). If stage durations are fixed (e.g., all individuals mature  
222 after two years as juveniles), then the goal is to create a “stage-for-age”  
223 model (e.g., Ebert) where the mean stage duration in the model equals the  
224 fixed stage duration in the life history. Even where real stage durations are  
225 somewhat variable, if there is a well-defined mean stage duration, then we  
226 can still aspire to have the modeled mean stage duration match the actual  
227 mean stage distribution.

228 Caswell (2001) has a section of his book describing various ways of doing  
229 this. It's not clear that there is a single “best” approach, as the stage-  
230 structured model will never match the age-structured model in all ways (see  
231 Discussion). Nevertheless, the primary analyses performed on most published  
232 MPMs are to calculate the asymptotic growth rate ( $\lambda$ ) and the sensitivity  
233 of  $\lambda$  to underlying demographic parameters. For these calculations, there  
234 is one (and only one) recipe to create a stage structured model that will  
235 generate the same results as the equivalent age-structured model with fixed  
236 stage durations. As best we can tell, it was first introduced by Caswell  
237 (1989), although its first application to an ecological population may have  
238 been by Crowder et al. (1994); it is covered in Caswell's (2001) section on  
239 stage-structured models.

240 The basic idea is that  $\gamma$  represents the fraction of individuals in the  
241 stage that have spent enough time in the stage to mature. This, in turn,  
242 depends on the (virtual) age structure within the stage. In general, this  
243 age structure could have any form, depending on the recent history of the  
244 population; the one time it is well defined is when the population is at the

245 stable age/stage distribution. This is exactly the condition for calculating  $\lambda$ .  
 246 Under these conditions, there are two factors that affect the age distribution  
 247 within the stage, and hence the fraction of individuals of an appropriate  
 248 age to mature. The first is the stage-specific survival, which determines  
 249 how a cohort shrinks as it ages. The second is the population growth rate,  
 250 which determines the degree to which one year's entering cohort is larger  
 251 or smaller than the previous one. This makes  $\gamma$  non-trivial to calculate,  
 252 as the resulting formula involves  $\lambda$ , which can only be calculated once the  
 253 MPM has been constructed! The solution is an iterative approach: take  
 254 an initial guess of  $\lambda$ , calculate  $\gamma$  from the formula; calculate the dominant  
 255 eigenvalue of the resulting matrix; use that as a new guess for  $\lambda$ ; and repeat  
 256 until the value of  $\lambda$  stops changing. For someone used to programming, this  
 257 is straightforward to implement; but non-modellers find this daunting, and  
 258 we do not know of any programs that implement this algorithm, aside from  
 259 some difficult-to-generalize Matlab code in Morris and Doak (2002). **Check**  
 260 **this out**

261 Thus, non-modellers will be tempted by easier-to-calculate formulas.  
 262 Some discover a predecessor to the above formula (Crouse et al., 1987)  
 263 that had been developed for the same population studied by Crowder et al.  
 264 (1994). This formula is complex-looking but straightforward to calculate, as  
 265 it doesn't require iteration (it incorporates the within-cohort dynamics, but  
 266 *assumes* that  $\lambda = 1$ ). An even simpler approach is to simply say that, if  
 267 the stage duration is  $T$  timesteps, then the fraction maturing is  $1/T$ . This  
 268 effectively assumes that the age distribution is perfectly flat. Its popularity  
 269 probably stems not just from the fact that it is simple to calculate and  
 270 explain, but because it is the first solution to the problem listed by Caswell  
 271 (2001), who seems to endorse it. **Check Caswell's actual wording**

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

### 277 3. Consequences of incorrect MPM construction

278 We evaluate the impacts of these errors in MPM construction by ex-  
 279 amining several endpoints that many analyses focus on: the asymptotic  
 280 population growth rate ( $\lambda$ ), sensitivity analysis of  $\lambda$  to changes in underlying  
 281 vital rates, and life history statistics such as generation time. We approach

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

296 *3.1. Effects on asymptotic population growth rate ( $\lambda$ )*

297 *3.2. Effects on sensitivity analysis of  $\lambda$*

298 *3.3. Effects on life history statistics*

## 299 **4. Prevalence of construction errors in published MPMs**

### 300 *4.1. Methods*

301 Sampling of COMADRE/COMPADRE

302 Questions related to fertility

303 Questions related to first reproduction

304 Questions related to maturation

305 Statistical analysis: means, trends through time

### 306 *4.2. Results*

307 Fertility

308 First reproduction

309 Maturation

## 310 **5. Discussion**

311 Summary of impacts

312 Summary of prevalence

313 Why does this happen? Most texts are incomplete (especially for stage-  
 314 structured models) and/or have inconsistent or confusing notation. Pick on  
 315 Caswell as example. Also, these are “threshold concepts.”

316 Recommendations for practitioners:

1. Use prebreeding census whenever possible
2. Unroll developmental stages (address sensitivity analysis challenges raised by Fujiwara and Diaz-Lopez, p. 2: “The inclusion of a large number of age-classes for long-lived organisms can make the interpretation of the sensitivity and elasticity analyses complicated because individuals in multiple age classes are often practically identical but separated in an age-structured model. Consequently, when long-lived organisms are studied, it is common to convert age-specific vital rates into stage-specific vital rates, and to use stage-structured population matrices for calculating  $\lambda$  and generation time.”)

Recommendations for experts:

1. Develop handbooks and training materials that are both comprehensive and clear to novices (reference threshold concepts)
2. Develop software tools to help guide practitioners through the process of translating demographic information in to MPMs

Revisiting prior results

- Individual studies
- Syntheses

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