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A model of inter-cohort cannibalism and paedomorphosis in Arizona Tiger Salamanders, *Ambystoma tigrinum nebulosum*

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Cannibalism is widespread in size-structured populations. If cannibals and victims are in different life stages, dominant cohorts of cannibals can regulate recruitment. Arizona Tiger Salamanders, *Ambystoma tigrinum nebulosum*, exhibit facultative paedomorphosis in which salamander larvae either metamorphose into terrestrial adults or become sexually mature while still in their larval form. Although many salamanders exhibit cannibalism of larvae, the Arizona Tiger Salamander also exhibits cannibalism of young by the aquatic adults. We formulate a differential equations model of this system under the assumption that the terrestrial adults do not impact the system beyond their contribution to the birth of young larvae. We establish non-negativity, boundedness and persistence of the salamander population under certain assumptions. We consider the equilibrium states of the system in the presence or absence of a birth contribution from the terrestrial or metamorph adults. Constant per capita paedomorphosis leads to asymptotically stable equilibria. The per capita paedomorphosis rate of the larvae must be density dependent in order for periodic solutions to exist. Furthermore, the stage transition rate must be sufficiently decreasing in order to guarantee the existence of an unstable equilibrium. Periodic solutions are only possible in the presence of a unique non-trivial unstable equilibrium. Our results conform to previous theory on paedomorphosis which suggests general applicability of our results to similar systems.

Keywords: Cannibalism; size-structured population; facultative paedomorphosis; population model; equilibrium analysis.

Mathematics Subject Classification 2010: 92D25, 92D40

1. Introduction

Cannibalism is widespread in size-structured populations where it has consequences for population, community, and food web dynamics [3, 15–19, 29, 30]. When cannibals and victims are in different age classes or life stages (e.g. adults and larvae), dominant cohorts of cannibals can regulate recruitment [11, 12, 14, 21]. Such is the case in size-structured, paedomorphic (branchiate adult) population of tiger salamanders, *Ambystoma tigrinum nebulosum.* Whether cannibalism from paedomorphs stabilizes or destabilizes populations likely depends on the interplay between the effects of cannibalism on paedomorph growth, fecundity, and the survival and growth of larval salamander victims [2, 13, 15]. It also may depend on factors such as the strength of competition between paedomorphs and larvae [8], and the sizes that determine which age classes of salamanders interact as cannibals and victims [3].

In this paper, we address these questions by modeling the dynamics of a paedomorphic tiger salamander population. Annual mark-recapture censuses at our main study site have documented salamander population fluctuations that are not correlated with interannual variation in climate or interactions with other species, parasites or pathogens [25, 28]. Rather, these fluctuations are associated with variation in the survival of young-of-the-year larvae [25]. Cannibalism by paedomorphic adults has been identified as the main driver of young-of-the-year mortality, reduced recruitment to the second year, and the resulting decline phase of observed population cycles [29].

2. Model Development

Our goal is to build a population model of the Arizona Tiger Salamanders found at our study site, the Mexican Cut Nature Preserve in Colorado. It is only possible to observe these salamanders during a brief portion of the year because of the Mexican Cut elevation. The salamanders are only accessible to field ecologists during part of the summer, which coincides with their breeding season. During this observation period, the salamanders are tagged by toe clips (before 2005) or PIT tags (since 2005). At this study site, it is possible for individual larvae to become sexually mature aquatic adults (paedomorphs) that retain their larval characteristics and aquatic life style [23, 25, 29]. At the same time, it is still possible for some of the Tiger Salamanders to metamorphose into sexually mature terrestrial adults (metamorphs) [7, 23].

There are several ponds at the Mexican Cut with different environmental conditions, some of which are permanent [26]. The isolation of the Mexican Cut allows us to assume that there are no migratory effects to/from the field site to be considered. We assume, for the purposes of this model, that the salamanders from the permanent ponds that exhibit paedomorphosis actually live in one pond surrounded by a closed land area in which the metamorphs live.

Discrete models have been studied extensively for size and stage-structured populations, see [1]. Delay equations and integro-difference equations have been used

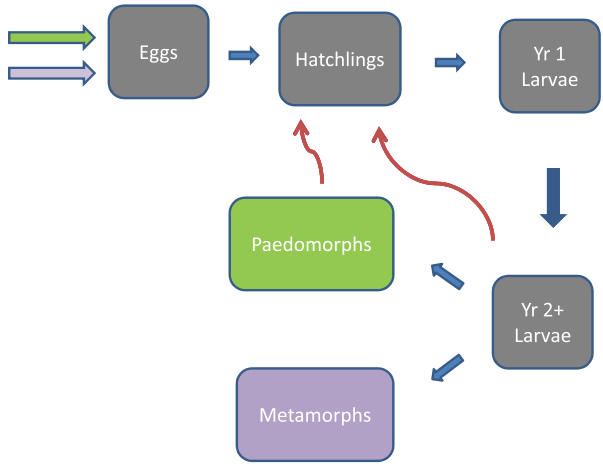

Fig. 1. (Color online) Arizona Tiger Salamander, *Ambystoma tigrinum nebulosum* life cycle with cannibalism. Egg contributions denoted by green (paedomorph) and purple (metamorph) arrows. Cannibalism of hatchlings by large larvae and paedomorphs denoted by red arrows. Progression through life cycle denoted by blue arrows.

to incorporate the lag between cohorts [4–6]. In this paper, we base our discussion on a classical compartment model using ordinary differential equations. This preliminary model does not incorporate delay, but instead looks for conditions that would support periodic solutions in the absence of a specific delay dependence.

We consider the stage-structured life cycle given by Fig. 1. Eggs $E(t)$ are laid in a pond by female paedomorphs or metamorphs. The eggs become young-of-the-year, $Y(t)$, also known as Year 0 larvae. The following season, the larvae that have survived are referred to as Year 1 larvae $L_1(t)$. Any summer after that, if the larvae is still alive, it is referred to as Year 2+ larvae, $L_{2+}(t)$. It is possible for Year 2+ larvae to remain larvae for several seasons before becoming a paedomorph $P(t)$ or a metamorph $M(t)$. Paedomorphs remain in the pond and lay eggs approximately every 2.4 years once they are approximately 10 years old [24]. Metamorphs leave the pond, but return approximately every 1.9 years to lay eggs once they are approximately 10 years old [25]. In addition to the standard logistic growth patterns that would be expected in a closed area, the paedomorphs and the Year 2+ larvae cannibalize the young-of-the-year [29].

We expect a general system of differential equations representing this life cycle to take the following form:

$$\frac{dE}{dt} = \text{laying of eggs}(M, P) - \text{transition}(E, Y) - \text{natural death},$$

$$\frac{dY}{dt} = \text{transition}(E, Y) - \text{transition}(Y, L_1) - \text{hatchling-cannibalism}(Y, L_2, P) - \text{natural death},$$

$$\frac{dL_1}{dt} = \text{transition}(Y, L_1) - \text{transition}(L_1, L_2) - \text{natural death},$$

$$\frac{dL_2}{dt} = \text{transition}(L_1, L_2) - \text{paedomorphosis}(L_2, P) - \text{metamorphosis}(L_2, M) - \text{natural death},$$

$$\frac{dP}{dt} = \text{paedomorphosis}(L_2, P) - \text{natural death},$$

$$\frac{dM}{dt} = \text{metamorphosis}(L_2, M) - \text{natural death}.$$

In order to simplify the model, we impose a size-based structure by defining two subgroups of the population as in Fig. 2. We group the eggs, young-of-the-year, and small or young larvae into a class that we represent by $L = E+Y+L_1$. We represent the larger or older larvae and the paedomorphs by $P = L_2 + P$. We note that the large larvae and paedomorphs cannibalize the young. It is not possible to count egg or hatchling populations directly. Instead, egg counts E are estimated via clutch size and reproductive frequency, while hatchling populations are estimated using an estimate of their probability of survival to young larvae L_1 and the L_1 population counts. The relative size of each of these groups is illustrated in Fig. 3 using data from [29]. The data suggest a periodic pattern in the relationship between L and P.

Paedomorphs typically spend all of their lives in the pond, while metamorphs leave for extended periods returning only to breed [7, 23]. In this paper, we shall ignore the metamorphs except for their contribution to the birth of the young larvae.

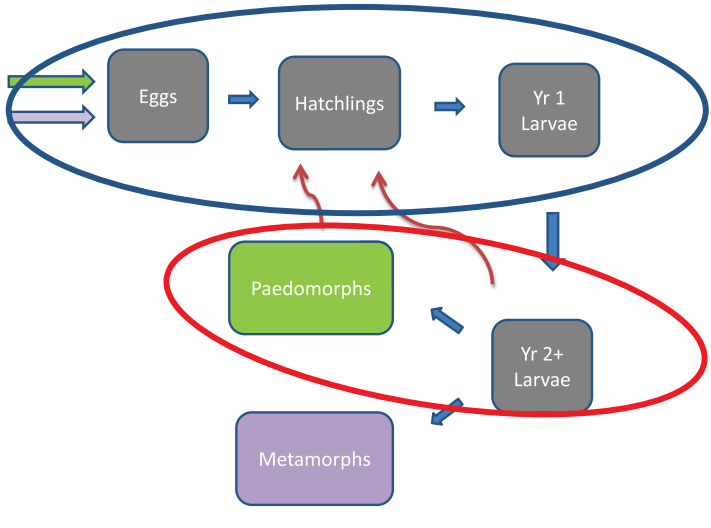

Fig. 2. Simplified life cycle model. Eggs, young-of-the-year, and small or young larvae form the first class (L). Larger or older larvae and the paedomorphs form the second class (P).

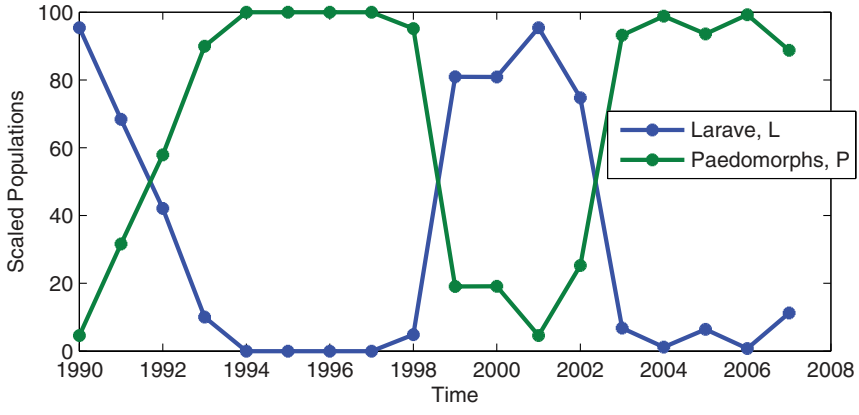

Fig. 3. Relative populations of larvae L and paedomorph P groups based on data from [29]. Egg counts estimated via clutch size and reproductive frequency. Young-of-the-year populations estimated using probability of survival to young larvae and Year 1+ population counts.

We expect a system of differential equations to take the following form:

$$\frac{dL}{dt} = \beta_0(t) + \beta_1(L,P)P - \mu(L,P)L - f(L,P)L,$$
$$\frac{dP}{dt} = f(L,P)L - \alpha(L,P)P.$$

In this system, $\beta_0(t)$ is the contribution to the larval population due to the metamorphs. $\beta_1(L,P)$ is the per capita reproduction rate of paedomorphs. $\mu(L,P)$ is the per capita mortality rate of larvae which can be due to natural death or cannibalism. $f(L,P)$ is the per capita rate of paedomorphosis of larvae and $\alpha(L,P)$ is the per capita mortality rate of paedomorphs. We assume that β_0 is a non-negative bounded continuous function. $\alpha, \beta_1 > 0$ and μ, f are all strictly positive bounded continuous functions on $[0,\infty)$ with continuous bounded derivatives on $(0,\infty)$.

Ignoring logistic effects in this paper, we discuss two possible larval birth terms. In the first, we ignore the contribution of the metamorphs and assume that $\beta_0(t) = 0$ and the per capita birth rate β_1 is constant. Later in the paper, we will incorporate the metamorph contribution to the larval birth with $\beta_0(t) \neq 0$ and β_1 constant.

We assume that the cannibalism term is linearly dependent on the earlier life stage. Hence $\mu(L,P)$ is independent of L. Typically, the consumption of L by P can be modeled by a Holling II consumption curve. This means that $\mu(L,P)$ is an increasing function of P.

It is well documented that the young-of-the-year and small larvae in the group L eat zooplankton and small invertebrates [27]. The large larvae and paedomorphs represented by P eat mostly large invertebrates and young-of-the-year. Since the competition between L and P for food can be neglected, we can assume that $f(L,P)$ is independent of P. The average length of the juvenile stage with death neglected

is $1/f(L)$. The time to paedomorphosis is either constant or increases with L, which means that $f(L)$ is a positive constant or a decreasing function of L.

The vast majority of paedomorphs in our main study population experience natural death due to either winter kill or old age [10, 25, 26]. Hence we assume that α is constant.

Under these assumptions, our model becomes

$$\begin{aligned} \frac{dL}{dt} &= \beta_0(t) + \beta_1 P - \mu(P)L - f(L)L, \\ \frac{dP}{dt} &= f(L)L - \alpha P \end{aligned} \tag{2.1}$$

with initial conditions $L(0) = L_0$ and $P(0) = P_0$.

3. Solution Properties and Existence of Equilibria

There is a trivial equilibrium only in the case $\beta_0(t) \equiv 0$. The existence of other equilibria depends on the following properties of the solutions.

Theorem 3.1. *For positive initial conditions $L(0) = L_0 > 0$ and $P(0) = P_0 > 0$, the system* (2.1) *has unique non-negative solutions that are bounded over finite time intervals.*

Proof. Recall our assumptions that β_0 is a non-negative bounded continuous function, $\alpha, \beta_1 > 0$ and $\mu(P), f(L)$ are all strictly positive bounded continuous functions on $[0, \infty)$ with continuous bounded derivatives on $(0, \infty)$. This gives existence and local uniqueness of solutions [20].

Consider first $\beta_0(t) > 0$. Starting with positive initial conditions, suppose that there exists $t_1 > 0$ such that $L(t_1) = 0$ but $P(t)$ is still positive. Since $L'(t_1) = \beta_0(t_1) + \beta_1 P(t_1) > 0$, the solution $L(t)$ must increase and become positive again. A similar argument applies if $P(t)$ reaches zero while $L(t) > 0$. If L and P reach zero simultaneously, at t_2 say, $\beta_0(t) > 0$ for some $t \geq t_2$ forces both solutions to become positive again.

If $\beta(t) \equiv 0$, the solutions are positive unless both become zero simultaneously in which case they remain at the trivial equilibrium $(0, 0)$. Thus we have unique non-negative solutions if either L_0 or P_0 is positive.

Let $N = L + P$ and suppose that $\beta_2 > \beta_0(t)$. Then

$$N' = \beta_0(t) + \beta_1 P - \mu(P)L - \alpha P < \beta_2 + \beta_1 N.$$

It follows that

$$N(t) < \frac{(\beta_2 + \beta_1(L_0 + P_0))e^{\beta_1 t} - \beta_2}{\beta_1}.$$

Therefore $L(t)$ and $P(t)$ are both bounded for finite time. □

The reproduction ratio $\mathcal{R}$ is the average number of offspring produced by a typical individual during its life. This is the product of the number of offspring produced by one paedomorph times the probability of surviving to be a paedomorph. For this model,

$$\mathcal{R}(L,P) = \left(\frac{\beta_0}{\alpha P} + \frac{\beta_1}{\alpha}\right)\left(\frac{f(L)}{\mu(P)+f(L)}\right).$$

In the absence of a metamorph birth contribution (i.e. $\beta_0 \equiv 0$), we define the basic reproduction ratio $\mathcal{R}_0$ as the average number of offspring produced by a typical individual in the absence of intraspecies competition or

$$\mathcal{R}_0 = \frac{\beta_1}{\alpha}\left(\frac{f(0)}{\mu(0)+f(0)}\right).$$

Corollary 3.2. *If $\beta_0(t)$ is constant and $\mathcal{R}_0 < 1$, the total population dies out. If $\mathcal{R}_0 > 1$, the total population is uniformly persistent.*

Proof. The result follows from an application of Thieme's Theorem 11.4 given in [20]. □

The existence of nontrivial equilibria requires assumptions on the ratio β_1/α. Recall that $\mu(P)$ is a continuous positive increasing function of P and $f(L)$ is a continuous positive nonincreasing function of L. Let $\mu_{\inf}, \mu_{\sup}, f_{\inf}, f_{\sup}$ denote the infima and suprema of μ and f.

Theorem 3.3. *If $\beta_0(t) \equiv \beta_0 \geq 0$ and*

$$1 + \frac{\mu_{\inf}}{f_{\sup}} \leq \frac{\beta_1}{\alpha} \leq 1 + \frac{\mu_{\sup}}{f_{\inf}},$$

then at least one positive equilibrium exists.

Proof. At an equilibrium (L^*, P^*), we must have $\mathcal{R}(L^*, P^*) = 1$ or

$$\frac{\beta_0}{\alpha P} + \frac{\beta_1}{\alpha} = 1 + \frac{\mu(P^*)}{f(L^*)}.$$

If $\beta_0 = 0$ the result follows from continuity of $\mu(P)$ and $f(L)$. If $\beta_0 > 0$, the continuity of $\mu(P)$ and $f(L)$ and the fact that $\lim_{P\to\infty} \beta_0/P = 0$ imply that for every $\varepsilon > 0$ there exists a $\tilde{P}$ such that

$$1 + \frac{\mu_{\inf}}{f_{\sup}} \leq \frac{\beta_0}{\alpha P} + \frac{\beta_1}{\alpha} \leq 1 + \frac{\mu_{\sup}}{f_{\inf}},$$

for all $P > \tilde{P}$. Thus for every L^* there exists at least one corresponding P^* giving an equilibrium pair (L^*, P^*), and vice versa. □

4. Equilibrium Analysis and Periodicity

4.1. *No metamorph contribution to birth rate*

We examine first the equilibria in the absence of a metamorph contribution to the larval birth rate. In this case our model becomes

$$\begin{aligned} \frac{dL}{dt} &= \beta_1 P - \mu(P)L - f(L)L, \\ \frac{dP}{dt} &= f(L)L - \alpha P. \end{aligned} \tag{4.1}$$

The associated Jacobian of (4.1) is

$$J(L,P) = \begin{pmatrix} -\mu(P) - f(L) - f'(L)L & \beta_1 - \mu'(P)L \\ f(L) + f'(L)L & -\alpha \end{pmatrix}.$$

At an equilibrium (L^*, P^*), we have

$$\operatorname{trace} J(L^*, P^*) = -\mu(P^*) - f(L^*) - f'(L^*)L^* - \alpha$$

and

$$\begin{aligned} \det J(L^*, P^*) &= \alpha\mu(P^*) + \alpha f(L) + \alpha f'(L^*)L^* - \beta_1 f(L^*) - \beta_1 f'(L^*)L^* \\ &\quad + f(L^*)\mu'(P^*)L^* + f'(L^*)\mu'(P^*)\,(L^*)^2 \\ &= f'(L^*)L^*[\alpha - \beta_1 + \mu'(P^*)L^*] + f(L^*)\mu'(P^*)L^*. \end{aligned}$$

The trivial or zero equilibrium $(L^*, P^*) = (0,0)$ gives

$$\operatorname{trace} J(0,0) = -\mu(0) - f(0) - \alpha < 0.$$

Since $\mathcal{R}_0 > 1$,

$$\det J(0,0) = \alpha\mu(0) + \alpha f(0) - \beta_1 f(0) < 0.$$

Therefore the zero equilibrium is an unstable saddle point.

Constant $f(L)$ ensures that a nonzero equilibrium is locally asymptotically stable because $\det J(L^*, P^*) > 0$. For nonincreasing $f(L)$, it is possible to construct equilibria of various types. Since $\mu(P)$ is increasing, we can write $\mu_{\inf} \le \mu(P) \le \mu_{\sup}$. If $f + f'(L^*)L^* > -\mu_{\inf} - \alpha$ and $\mu'(P^*)L^* < \beta_1 - \alpha$, then $\operatorname{trace} J(L^*, P^*) < 0$ and $\det J(L^*, P^*) > 0$ yielding an equilibrium that is locally asymptotically stable.

If $f + f'(L^*)L^* < -\mu_{\sup} - \alpha$, then $\operatorname{trace} J(L^*, P^*) > 0$ which guarantees that the equilibrium is unstable. We note that, in this case, the stage transition rate $Lf(L)$ is decreasing, indicating strong negative feedback from the number of juveniles [20].

Ultimately, the nature of the equilibrium is characterized by the relationship between the stage transition rate $(fL)'$ and the bounds on the per capita mortality rate $\mu(P)$. In particular, a large lower bound on the per capita larvae mortality, $\mu_{\inf}$, guarantees stability for any nontrivial equilibrium. A small upper bound on the per capita larvae mortality, $\mu_{\sup}$ allows for possible instability of a nontrivial unstable equilibrium.

4.2. *Constant metamorph contribution*

If there is a constant metamorph contribution to the birth rate then $\beta_0(t) = \beta_0$ for some constant $\beta_0 > 0$. In this case our model becomes

$$\begin{aligned} \frac{dL}{dt} &= \beta_0 + \beta_1 P - \mu(P)L - f(L)L, \\ \frac{dP}{dt} &= f(L)L - \alpha P. \end{aligned} \tag{4.2}$$

It is obvious that there is no trivial equilibrium in this case.

The Jacobian of the system has not changed, but the equilibrium condition is now

$$\frac{\beta_0}{\alpha P} + \frac{\beta_1}{\alpha} = 1 + \frac{\mu(P)}{f(L)}.$$

Hence

$$\operatorname{trace} J(L^*, P^*) = -\mu(P^*) - f(L^*) - f'(L^*)L^* - \alpha$$

and

$$\begin{aligned} \det J(L^*, P^*) &= \alpha\mu(P^*) + \alpha f(L) + \alpha f'(L^*)L^* - \beta_1 f(L^*) - \beta_1 f'(L^*)L^* \\ &\quad + f(L^*)\mu'(P^*)L^* + f'(L^*)\mu'(P^*)(L^*)^2 \\ &= f'(L^*)L^*[\alpha - \beta_1 + \mu'(P^*)L^*] + f(L^*)[\beta_0/P^* + \mu'(P^*)L^*] \end{aligned}$$

at an equilibrium (L^*, P^*).

Constant $f(L)$ ensures that a nonzero equilibrium is locally asymptotically stable because $\det J(L^*, P^*) > 0$. For nonincreasing $f(L)$, it is possible to construct equilibria of various types.

If $f + f'(L^*)L^* > -\mu_{\inf} - \alpha$ and $\mu'(P^*)L^* < \beta_1 - \alpha$, then $\operatorname{trace} J(L^*, P^*) < 0$ and $\det J(L^*, P^*) > 0$ yielding an equilibrium that is locally asymptotically stable. If $f + f'(L^*)L^* < -\mu_{\sup} - \alpha$, then $\operatorname{trace} J(L^*, P^*) > 0$, we have an unstable equilibrium because $\operatorname{trace} J(L^*, P^*) > 0$. There is also strong negative feedback from the number of juveniles in this case [20].

Once again, the nature of the equilibrium is characterized by the relationship between the stage transition rate $(fL)'$ and the bounds on the per capita mortality rate $\mu(P)$.

4.3. *Periodicity*

Since our solutions are non-negative and bounded, if there is only one nonzero equilibrium and it is unstable, the Poincaré–Bendixson theorem implies that there must be at least one closed periodic orbit [9]. Periodic solutions are not possible when $f(L)$ is constant. This is consistent with the biological literature which shows that density dependence of the paedomorphosis rate $f(L)$ is necessary for the existence of periodic solutions [7, 23, 26].

5. Example

Consider a decreasing per capita paedomorphosis rate $f(L) = f_0 e^{-kL}$ where k and f_0 are positive constants. This function is negatively density-dependent which is consistent with what is noted in the biological literature [7, 23, 26].

We consider also an increasing per capita mortality rate of larvae

$$\mu(P) = \mu_1 + \frac{(\mu_2 - \mu_1)P}{P + b},$$

where μ_1, μ_2 and b are positive constants. We note that μ_1 is the natural death rate and the second term in $\mu(P)$ represents the cannibalism of the larvae by the paedomorphs.

In the absence of a metamorph contribution to the birth rate (i.e. $\beta_0 \equiv 0$), the equilibrium condition can be written as

$$\left(\frac{\beta_1}{\alpha} - 1\right) f(L) = \mu(P).$$

Application of Theorem 3.3 yields an existence condition

$$1 + \frac{\mu_1}{f_0} \leq \frac{\beta_1}{\alpha} < \infty. \tag{5.1}$$

After some calculations, we find that

$$\text{trace}\,(J) = -\frac{\beta_1}{\alpha} f(L) - f'(L)L - \alpha = f_0 e^{-kL}\left(kL - \frac{\beta_1}{\alpha}\right) - \alpha$$

and

$$\begin{aligned}\det(J) &= f'(L)L(\alpha - \beta_1) + \mu'(P)L(f(L)L)' \\ &= f_0 e^{-kL} L\left(k(\beta_1 - \alpha) + \frac{(\mu_2 - \mu_1)b}{(P+b)^2}(kL - 1)\right).\end{aligned}$$

If $1 < kL < \beta_1/\alpha$ then $\text{trace}\,(J) < 0$ and $\det(J) > 0$ yielding a locally asymptotically stable equilibrium.

On the other hand, if

$$kL > \frac{\beta_1}{\alpha} + \frac{\alpha}{f_0} e^{kL}, \tag{5.2}$$

we can show that $\text{trace}\,(J) > 0$ forces an unstable equilibrium. Thus, for a certain range of L, all equilibrium pairs (L^*, P^*) will be unstable. In this case, periodic solutions are possible. We note that, for this particular example, the instability condition (5.2) depends explicitly on the per capita rate of paedomorphosis of larvae into paedomorphs, via the constant f_0. It is indirectly dependent on the per capita mortality rate of larvae, via the constant μ_1 which appears in the equilibrium existence condition (5.1).

6. Discussion

We have constructed a general ordinary differential equation model for the production of cannibalistic paedomorphic Arizona Tiger Salamanders, *Ambystoma tigrinum nebulosum*. With the exception of their contribution to the birth term, we ignore the interactions of the metamorphs with the larvae and paedomorphs. A closer study of this aspect will be the subject of a later paper. This preliminary model does not explicitly incorporate delay effects. Rather, we determine conditions that support periodic solutions in the absence of a specific delay dependence.

We have established conditions on the per capita paedomorphosis rate of the larvae $f(L)$ and the per capita mortality rate of the larvae $\mu(P)$ for the existence of equilibria. The per capita mortality rate $\mu(P)$ depends on natural death and inter-cohort cannibalism. The most significant aspects of this function are its upper and lower bounds. $\mu(P)$ is bounded below by the nonzero natural death rate μ_{inf} and it is this number and its relationship with $(Lf(L))'$ that determines local asymptotic stability for a nonzero equilibrium. The relationship between the upper bound μ_{sup} and $(Lf(L))'$ determines instability.

The paedomorphosis rate is more significant in the analysis. In particular, it must be density-dependent in order for periodic solutions to exist, which has been found in numerous studies (see reviews by [7, 23, 26]). Constant per capita paedomorphosis leads to asymptotically stable equilibria in the presence or absence of a metamorph birth contribution. Furthermore, the stage transition rate $Lf(L)$ must be sufficiently decreasing in order to guarantee the existence of an unstable equilibrium. Such a decreasing rate is expected under some theoretical scenarios. For example, one proposed mechanism for the production of new paedomorphs predicts negative density dependence [22, 23], and this mechanism has been shown to operate in a variety of salamander populations [7, 23, 26]. We consider an example of such negative density dependence. We note once again that periodic solutions are only possible in the presence of an unstable equilibrium which exists only in particular circumstances.

Future work will include the incorporation of logistic growth, positive feedbacks due to cannibalism and delay effects. We will also compare the death rates associated with cannibalism with natural death rates. Furthermore, we will consider a model with more size-classes and directly incorporate the contribution of metamorphs to the birth rate.

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References

[1] H. Caswell, *Matrix Population Models*: *Construction*, *Analysis*, *and Interpretation* (Sinauer Associates, Sunderland, MA, 2001).

[2] D. Claessen and A. M. de Roos, Bistability in a size-structured population model of cannibalistic fish: A continuation study, *Theor. Popul. Biol.* **64** (2003) 49–65.

[3] D. A. Claessen, A. M. de Roos and L. Persson, Population dynamic theory of size-dependent cannibalism, *Proc. Roy. Soc. B* **271** (2004) 333–340.

[4] J. M. Cushing, A size-structured model for cannibalism, *Theor. Popul. Biol.* **42** (1992) 347–361.

[5] J. M. Cushing, The dynamics of hierarchial age-structured populations, *J. Math. Biol.* **32** (1994) 705–729.

[6] J. M. Cushing, *An Introduction to Structured Population Dynamics* (Society for Industrial and Applied Mathematics, 1998).

[7] M. Denoël, P. Joly and H. H. Whiteman, Evolutionary ecology of facultative paedomorphosis in newts and salamanders, *Biol. Rev.* **80** (2005) 1–9.

[8] A. M. de Roos and L. Persson, Competition in size-structured populations: Mechanisms inducing cohort formation and population cycles, *Theor. Popul. Biol.* **63** (2003) 1–16.

[9] L. Edelstein-Keshet, *Mathematical Models in Biology* (Society for Industrial and Applied Mathematics, 2005).

[10] C. J. Eden, H. H. Whiteman, L. Duobinis-Gray and S. A. Wissinger, Accuracy assessment of skeletochronology in the Arizona Tiger Salamander (*Ambystoma tigrinum nebulosum*), *Copeia* **2007** (2007) 471–477.

[11] S. Gaines and J. Roughgarden, Larval settlement rate: A leading determinant of structure in an ecological community of the intertidal zone, *Proc. Natl. Acad. Sci.* (*USA*) **82** (1985) 3707–3711.

[12] A. Hastings and R. F. Costantino, Cannibalistic egg-larva interactions in *tribolium*: An explanation for the oscillations in population numbers, *Amer. Nat.* **130** (1987) 36–52.

[13] A. Hastings and R. F. Costantino, Oscillations in population numbers: Age-dependent cannibalism, *J. Anim. Ecol.* **60** (1991) 471–482.

[14] E. F. McCauley and W. W. Murdoch, Cyclic and stable populations: Plankton as a paradigm, *Amer. Nat.* **129** (1987) 97–121.

[15] L. Persson, D. Claessen, A. M. de Roos, P. Byström, S. Sjögren, R. Svanbäck and E. Westman, Cannibalism on a size-structured population: Energy extraction and control, *Ecol. Monogr.* **74** (2004) 135–157.

[16] L. Persson, A. M. de Roos and A. Bertolo, Predicting shifts in dynamics of cannibalistic field populations using individual-based models, *Proc. Roy. Soc.* **271** (2004) 2489–2493.

[17] V. H. W. Rudolf, Consequences of stage-structured predators: Cannibalism, behavioral effects, and trophic cascades, *Ecology* **88** (2007) 2992–3003.

[18] V. H. W. Rudolf, The interaction of cannibalism and omnivory: Consequences for community dynamics, *Ecology* **88** (2007) 2697–2705.

[19] V. H. W. Rudolf, Impact of cannibalism on predator–prey dynamics: Size-structured interactions and apparent mutualism, *Ecology* **89** (2008) 1650–1660.

[20] H. R. Thieme, *Mathematics in Population Biology* (Princeton University Press, 2003).

[21] J. Van Buskirk, Competition, cannibalism, and size-class dominance in a dragonfly, *Ecology* **65** (1992) 455–464.

[22] J. Y. Wakano and H. H. Whiteman, Evolution of polyphenism: The role of density and relative body size in morph determination, *Evol. Ecol. Res.* **10** (2008) 1157–1172.

[23] H. H. Whiteman, Evolution of facultative paedomorphosis in salamanders, *Quart. Rev. Biol.* **69** (1994) 205–221.
[24] H. H. Whiteman, Maintenance of polymorphism promoted by sex-specific fitness payoffs, *Evolution* **51** (1997) 2039–2044.
[25] H. H. Whiteman and S. A. Wissinger, Amphibian population cycles and long-term datasets, in *Amphibian Declines*: *Conservation Status of US Species*, ed. M. L. Lanoo (California University Press, 2005).
[26] H. H. Whiteman, S. A. Wissinger, M. Denoël, C. J. Mecklin, N. M. Gerlanc and J. J. Gutrich, Larval growth in polyhenic salamanders: Making the best of a bad lot, *Oecologia* **168** (2012) 109–118.
[27] S. A. Wissinger, A. J. Bohonak, H. H. Whiteman and W. S. Brown, Subalpine wetlands in Colorado: Habitat permanence, salamander predation and invertebrate communities, in *Invertebrates in Freshwater Wetlands of North America*: *Ecology and Management*, eds. D. P. Bazter and S. A. Wissinger (John Wiley and Sons, 1999).
[28] S. A. Wissinger and H. H. Whiteman, Fluctuation in a Rocky Mountain population of salamanders: Anthropogenic acidification or natural variation? *J. Herpetol.* **26** (1992) 377–391.
[29] S. A. Wissinger, H. H. Whiteman, M. Denoël, M. L. Mumford and C. B. Aubee, Consumptive and nonconsumptive effects of cannibalism in fluctuating age-structured populations, *Ecology* **91** (2010) 549–559.
[30] G. Woodward, D. C. Speirs and A. G. Hildrew, Quantification and temporal resolution of a complex size-structured food web, *Adv. Ecol. Res.* **36** (2005) 85–135.