OSCILLATIONS IN A SIZE-STRUCTURED PREY-PREDATOR MODEL

SOUVIK BHATTACHARYA AND MAIA MARTCHEVA*

Abstract. This article introduces a predator-prey model with the prey structured by body size, based on reports in the literature that predation rates are prey-size specific. The model is built on the foundation of the one-species physiologically structured models studied earlier. Three types of equilibria are found: extinction, multiple prey-only equilibria and possibly multiple predator-prey coexistence equilibria. The stabilities of the equilibria are investigated. Comparison is made with the underlying ODE Lotka-Volterra model. It turns out that the ODE model can exhibit sustain oscillations if there is an Allee effect in the net reproduction rate, that is the net reproduction rate grows for some range of the prey's population size. In contrast, it is shown that the structured PDE model can exhibit sustain oscillations even if the net reproductive rate is strictly declining with prey population size. We find that predation, even size-nonspecific linear predation can destabilize a stable prey-only equilibrium, if reproduction is size specific and limited to individuals of large enough size. Furthermore, we show that size-specific predation can also destabilize the predator-prey equilibrium in the PDE model. We surmise that size-specific predation allows for *temporary* prey escape which is responsible for destabilization in the predator-prey dynamics.

Keywords: predator, prey, physiological structure, individual size, oscillations, Lotka-Volterra model, predator escape mechanism

1. Introduction

Predator-prey interactions have fascinated mathematical biologists for a long time. Several long-term data sets have been collected for predator and prey interactions in nature. The most well-known one between the lynx and its prey, the hair, is now discussed in many mathematical biology textbooks [1]. These data sets have suggested that the predator-prey interactions in nature often persist in the form of oscillations. The question what accounts for the periodicity in the predator-prey dynamics has been a central question in mathematical biology for many years leading to a multitude of articles discussing oscillations in ordinary differential equation models [11]. *In this article we set forth the hypothesis that predation and prey individuals' differential body size may be responsible for the oscillations observed in the predator-prey interactions in nature.*

The interactions between the predator and the prey are strongly influenced both by the size of the predator and the size of the prey [13]. Biological literature abounds with articles discussing the role of size in predator-prey interactions in a variety of natural systems [12]. Yet, the role of size, as a continuous variable, in the context of predator-prey models, has rarely been discussed in the mathematical biology literature. De Roos

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*author for correspondence.

at al investigate the role of food availability on the size of the predator *Daphnia* and find that there is coexistence in a stable equilibrium, and stable cycles [10]. In [10] the authors find that destabilization occurs if the prey population can escape the control, imposed by the predator. In this article we take the opposite perspective: we look at the impact of the size of the prey on the predator-prey interaction and we surmise that the presence of *temporary* prey escape mechanism may still be responsible for the destabilization of the dynamics. The main question we address is whether size-specific predation by the predator can be responsible for the oscillations in the predator-prey dynamics.

Our size-structured prey-predator partial differential equation model is based on the non-linear single-population size structured model investigated in [2]. Our investigation is motivated by reports in the biological literature that predators prefer prey of certain body size, while the body size of all preys may vary in a large range [3]. It has been suggested that predators tend to prefer medium-size prey as too large prey may be too difficult to handle, while too small prey may be too challenging to catch. However, if adequate refuge is available, then the predation rate declines with the size of the prey [6]. The question whether prey size may be a destabilizing factor in the predator-prey interactions seems an open and interesting question that we address here.

Oscillations based on size-structure in prey and predator, investigated through ordinary differential equations, have been found in pelagic ecosystem models [5]. Mathematically, our results parallel most closely the investigation of a predator-prey model which accounts for prey age-structure [4]. Li finds, just as we do, three types of equilibria: an extinction equilibrium, a prey-only equilibrium, and a coexistence equilibrium, and performs partial analysis of their stabilities. A more general model in which both the predator and the prey are physiologically structured is introduced by Logan *et al.* [8] (see also [7]). However, such a model is rather complex, and the authors consider a number of more tractable special cases. In contrast with their model, which includes a Holling II functional response, our only includes a linear size-dependent functional response. Our reason for accounting only for linear functional response is to eliminate the possibility that the Holling functional response, well known to destabilize predator-prey interactions, had destabilized the coexistence equilibrium. With linear functional response, and monotone decreasing recruitment rate, the underlying ODE model of our PDE system will not exhibit oscillations.

In this article, we discuss a predator-prey model, where the prey is physiologically structured by a continuous variable, called size. The model is introduced in section two. Section two also takes a look at the homogenous predator-prey ODE model, allowing us later to focus on the effects generated by the presence of size-structure. Section three investigates the equilibria. The first subsection focuses on the prey-only equilibria, while the second subsection investigates the coexistence equilibria. Section four performs stability analysis. Again, the first subsection focuses on the local stability of the extinction equilibrium, the second subsection investigates the local stability of prey-only equilibria. The last subsection looks at the stability and the presence of Hopf bifurcation of a coexistence equilibrium. Section five summarizes our results.

2. A SIZE-STRUCTURED LOTKA-VOLTERRA TYPE PREDATOR-PREY MODEL

In this section we consider a size-structured population model introduced in the paper by Calsina and Saldaña [2]. The model is a non-linear first order partial differential equation, equipped with nonlocal boundary conditions. As we are interested in the size specific predation effects of a specialist predator we are going to extend that model to incorporate a predator population. The resulting extended model is a size-structured version of the well-known Lotka-Volterra predation model.

The model, as introduced in [2], describes the dynamics of the size-structured prey. It is presented below in notation consistent with our extended size-structured predator-prey model:

$$u_t + (g(x, N(t))u(x,t))_x + \mu(x, N(t))u = 0, x \in [0, \infty) \tag{2.1}$$

$$g(0, N(t))u(0,t) = \int_0^\infty \beta(x, N)u(x,t)dx, t > 0 \tag{2.2}$$

$$u(x, 0) = \phi(x), x \in [0, \infty) \tag{2.3}$$

where the total population size $N(t)$ at time t is given by:

$$N(t) = \int_0^\infty u(x,t)dx.$$

The function $u(x,t)$ represents the density of the prey population of size x and at time t. In particular that means that $\int_a^b u(x,t)dx$ represents the number of prey from size a to size b where both a and b are positive numbers. Here $\mu(x, N)$ represents the natural per capita size-dependent death rate. Furthermore, $\beta(x, N)$ gives the per capita size-dependent birth rate. The model assumes that all births occur to the same initial size which we have shifted to be zero. Both μ and β are nonnegative, Lipschitz continuous with respect to x and N functions. Furthermore, the birth and death rates satisfy:

ASSUMPTION 2.1. *The birth and death rate satisfy*

- $\lim_{N\to\infty} \beta(x, N) = 0$
- β *is a bounded function with respect to both* x *and* N*, that is,*
$$\sup_{x,N} \beta(x, N) = \bar{\beta}.$$
- $\beta(X, N)$ *is positive as a function of* x *on a set of positive measure.*
- μ *is bounded from below:*
$$\mu(x, N) \geq \underline{\mu}.$$

The function $g(x, N)$ is the growth rate. We assume it is a continuously differentiable function with respect to x. For the remainder of this work we will assume that $g(x, N)$ is, in fact, independent of N, that is $g(x, N) = g(x)$. Furthermore, $g > 0$ for all $x \in [0, \infty)$. The initial condition $\phi(x)$ is a non-negative and integrable function, which is positive on a set of positive measure.

In the present paper we include the effect of a specialist predator. The inclusion of a specialist predator introduces an additional variable and also an additional equation in the system. We assume the predator feeds on prey of specific size and denote the size-specific per capita predation rate by $\gamma(x)$. The predation rate $\gamma(x)$ is a bounded, Lipschitz continuous function. We assume that $\gamma(x) > 0$ on a set of positive measure. Denote by

$$\overline{\gamma} = \sup_x \gamma(x).$$

We incorporate the effect of predation as predator-introduced additional mortality on the prey which is size-dependent. The resulting model is given as follows.

$$\begin{aligned} u_t + (g(x)u(x,t))_x &= -\mu(x,N)u - \gamma(x)Pu, \\ g(0)u(0,t) &= \int_0^\infty \beta(x,N)u(x,t)dx, \\ u(x,0) &= \phi(x), P(0) = P_0, \\ P' &= P\int_0^\infty \alpha(x)\gamma(x)u(x,t)dx - dP. \end{aligned} \tag{2.4}$$

The time-dependent function $P(t)$ represents the total number of predators at time t. The parameter $\alpha(x)$ is the prey-size dependent predators' metabolic efficiency by which the biomass of consumed prey is transformed into predator's biomass. Finally, d is the death rate of predators. The total number of predators P is a nonnegative function. Predators' death rate d and metabolic efficiency $\alpha(x)$ are also nonnegative. The number of predators at time $t = 0$ is given by the nonnegative number P_0. The assumptions on the parameters above will be valid throughout the article and should guarantee well-posedness of the main model (2.4).

If we assume all rates independent of the prey size x, that is we assume $\beta(x,N) = \beta(N)$, $\mu(x,N) = \mu(N)$, $\gamma(x) = \gamma$, $\alpha(x) = \alpha$, then the size-structured model (2.4) collapses to the following ordinary differential equation Lotka-Volterra model:

$$\begin{aligned} N' &= (\beta(N) - \mu(N))N - \gamma PN, \\ P' &= \alpha\gamma PN - dP, \\ N(0) &= N_0, P(0) = P_0. \end{aligned} \tag{2.5}$$

This system has an extinction equilibrium $\mathcal{E}_0 = (0,0)$ in which both the predator and the prey populations go extinct. The extinction equilibrium is locally stable if $\beta(0) < \mu(0)$, and unstable otherwise. For the remainder of this section we will assume that $\beta(0) > \mu(0)$ so that at least the prey population is viable. In the absence of the predator, the prey-only equilibria are obtained as solutions to the equation

$$\beta(N) = \mu(N). \tag{2.6}$$

Assumptions (2.1) and the fact that $\beta(0) > \mu(0)$ imply that this equation has at least one positive solution N^*. However, equation (2.6) may have solutions even if $\beta(0) < \mu(0)$. Assume the equation has k solutions $N_1^*, \dots N_k^*$, all of which are simple solutions and ordered in increasing order (see Figure 1).

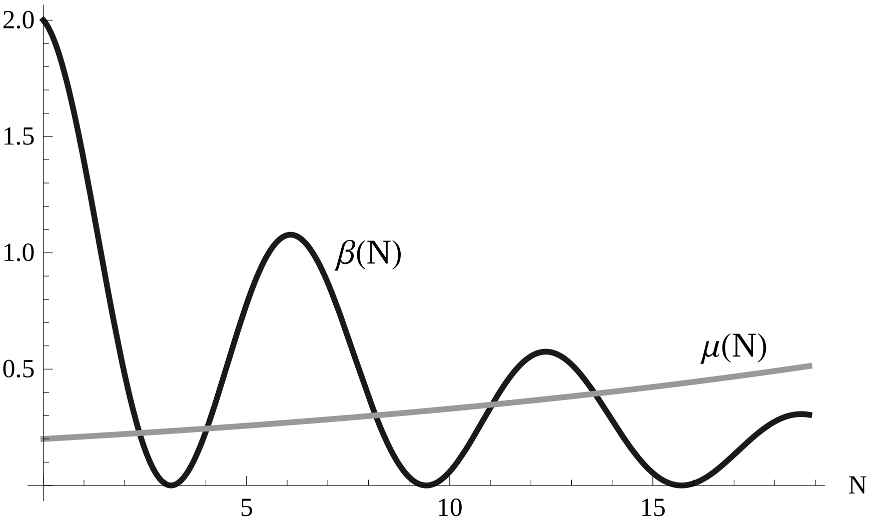

Figure 1. A graph of the functions $\beta(N)$ and $\mu(N)$. Each point of intersection of the two curves gives one solution to the equation $\beta(N) = \mu(N)$, and one prey-only equilibrium.

Each of these solutions gives a prey-only equilibrium $\mathcal{E}_j = (N_j^*, 0)$. Each of these equilibria is locally stable if

$$\beta'(N_j^*) < \mu'(N_j^*) \qquad \text{and} \qquad \alpha\gamma N_j^* - d < 0 \tag{2.7}$$

and unstable otherwise. The second inequality says that the predator cannot invade the $\mathcal{E}_j$'th equilibrium of the prey. Define the threshold quantity

$$\hat{N} = \frac{d}{\alpha\gamma}. \tag{2.8}$$

Clearly all prey-only equilibria $\mathcal{E}_j$ satisfying $N_j^* > \hat{N}$ are unstable. In other words, if the prey-only population is large enough, it will support the predator to exist. We call the quantity $\hat{N}$ *minimum threshold prey population size for existence of the predator*. Since equilibria are all simple, the inequality between the derivatives of β and μ changes with each equilibrium. For instance, on Figure 1, there are five solutions: $N_1^*, \ldots, N_5^*$. We have $\beta(N_1^*) < \mu(N_1^*)$, $\beta(N_2^*) > \mu(N_2^*)$, etc. If the minimum threshold prey population size for existence of predator is large enough, then prey-only equilibria N_1^*, N_3^*, N_5^* in Figure 1 will be locally stable.

System (2.5) has a unique coexistence equilibrium of the predator and the prey $\mathcal{E}^* = (\hat{N}, \hat{P})$ where $\hat{N}$ is given in (2.8), and $\hat{P} = (\beta(\hat{N}) - \mu(\hat{N}))/\gamma$. The coexistence equilibrium is locally stable if and only if

$$\beta'(\hat{N}) < \mu'(\hat{N}). \tag{2.9}$$

If (2.9) fails, the coexistence equilibrium may become destabilized and sustained oscillations are possible (see Figure 2). Hence, the simple predator-prey model in (2.5) is capable of complex behavior.

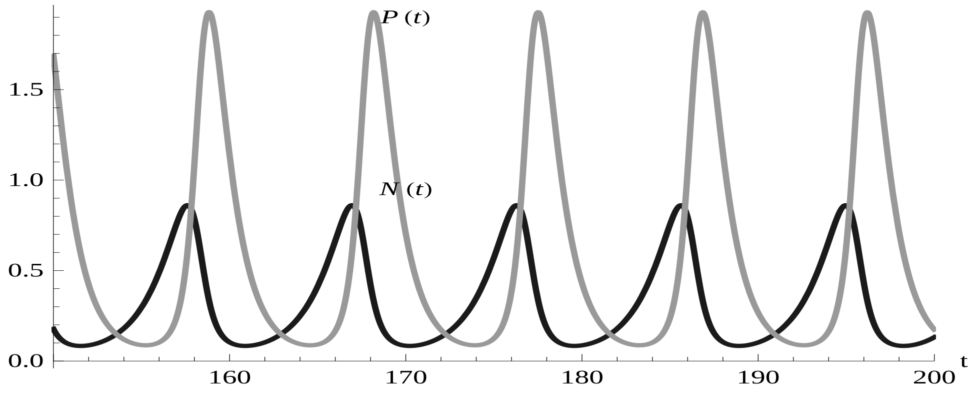

FIGURE 2. A graph of the functions $N(t)$ and $P(t)$. The graph shows oscillations in the numbers of the predator and the prey.

3. EQUILIBRIA OF THE SIZE-STRUCTURED PREDATOR-PREY MODEL

With the assumptions made in Section 2, existence and uniqueness of solutions to model (2.4) can be proved similarly as in [2]. In this section we are interested in time-independent solutions (equilibria) of the model (2.4). The system for the equilibria is

$$(g(x)u(x))_x = -\mu(x,N)u - \gamma(x)Pu, \tag{3.1}$$

$$g(0)u(0) = \int_0^\infty \beta(x,N)u(x)dx, \tag{3.2}$$

$$0 = P\int_0^\infty \alpha(x)\gamma(x)u(x)dx - dP, \tag{3.3}$$

where P is the total predator size at the equilibrium. The constant N represents the total prey size at the equilibrium and is given by:

$$N = \int_0^\infty u(x)dx.$$

Assuming that N and P are given constants, the differential equation for u (3.1) can be integrated

$$\begin{aligned} u(x) &= u(0)\frac{g(0)}{g(x)}e^{-\int_0^x(\frac{\mu(x,N)}{g(s)}+\frac{\gamma(s)}{g(s)}P)ds} \\ &= u(0)g(0)\pi(x,P,N) \end{aligned} \tag{3.4}$$

where for a fixed P and N we have introduced the following notation

$$\pi(x,P,N) = \frac{1}{g(x)}e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{\gamma(s)}{g(s)}Pds}.$$

The function π can be interpreted as the probability of the prey to survive till size x. To find $u(0)$, P and N we place the formula for $u(x)$ into the renewal equation, the equation for the predator, and the equation of the total prey size. We obtain the following nonlinear system of three equations in the unknowns $u(0)$, P and N.

$$\begin{aligned} g(0)u(0) &= u(0)g(0)\int_0^\infty \beta(x,N)\pi(x,P,N)dx, \\ 0 &= Pu(0)g(0)\int_0^\infty \alpha(x)\gamma(x)\pi(x,P,N)dx - dP, \\ N &= u(0)g(0)\int_0^\infty \pi(x,P,N)dx. \end{aligned} \tag{3.5}$$

An equilibrium solution of the system (2.4) is given by the triple $(u(0), P^*, N^*)$, where $u(0)$, P^*, and N^* are a solution of the system (3.5). System (3.5) always has the trivial solution where $u(0) = 0$, $P^* = 0$, $N^* = 0$. The triple $\mathcal{E}_0 = (0, 0, 0)$ gives the extinction equilibrium. Besides the extinction equilibrium, there are two types of other equilibria. The first type are predator-free equilibria, where the predator goes extinct but the prey population size persists. The second type of equilibria are coexistence equilibria where both predator and prey are present. We consider the following two cases.

3.1. **Prey-only equilibria.** In this case we have $P^* = 0$. Hence the equilibria here would be of the form $(u(0), 0, N^*)$. We have to find the values of $u(0)$ and N^*. With $P^* = 0$ system (3.5) takes the form

$$\begin{aligned} 1 &= \int_0^\infty \frac{\beta(x,N)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds} dx, \\ N &= \int_0^\infty u(0)\frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds} dx, \end{aligned} \tag{3.6}$$

where

$$u^*(x) = u(0)\frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds}. \tag{3.7}$$

The first equation in the system (3.6) is independent of the second equation and depends on N but not on $u(0)$. We can solve the first equation in system (3.6) for N. Then we obtain $u(0)$ from the second equation in system (3.6). Hence, given that we know N^*, we get

$$u(0) = \frac{N^*}{\int_0^\infty \frac{g(0)}{g(x)} e^{-\int_0^x \frac{\mu(x,N^*)}{g(s)}ds} dx}.$$

Therefore, system (3.6) is essentially a decoupled non-linear system. We note that since $g(0) > 0$ the denominator in the formula for $u(0)$ is nonzero. We now focus on the number of solutions of the first equation in (3.6).

We define the net reproduction rate as a function of the prey population size:

$$\mathcal{R}(N) = \int_0^\infty \frac{\beta(x,N)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds} dx. \tag{3.8}$$

The behavior of this function of N determines the mechanisms of growth of the prey population. To understand better the solutions of the equation $\mathcal{R}(N) = 1$ we assume some typical types of birth and death rate functions and then try to explore the existence of equilibria.

Assumption 3.1. *Assume the birth and death rates have the following properties:*

1. $\beta(x,N) = R_0\beta_0(N)\Phi(x)$, *where* $\Phi(x)$ *is a given function of* x *giving the reproductivity of different sizes of prey. In later examples* Φ *is taken to be the characteristic function of the sizes of prey, responsible for reproduction.*
2. $\mu(x,N) = \mu_0(N)+m(N)\Psi(x)$, $\Psi(x)$ *is a given function of* x*, giving the mortality of prey, based on size.*
3. $[\beta_0(0)]^{-1} = \int_0^\infty \frac{\Phi(x)}{g(x)} e^{-\int_0^x \frac{\mu(s,0)}{g(s)}ds} dx.$
4. *All functions and constants are nonnegative (positive).*

If Assumptions 3.1 hold, the equation for the total population size $\mathcal{R}(N) = 1$ takes the form

$$1 = \int_0^\infty \frac{R_0\beta_0(N)\Phi(x)}{g(x)} e^{-\int_0^x \frac{\mu_0(N)+m(N)\Psi(x)}{g(s)}} dx \tag{3.9}$$

We have to prove that there exists an N that satisfies equation (3.9). For $N = 0$ we have by the Assumptions 3.1 above

$$\mathcal{R}(0) = R_0$$

We call R_0 intrinsic reproduction number of the prey population. In what follows we consider specific examples.

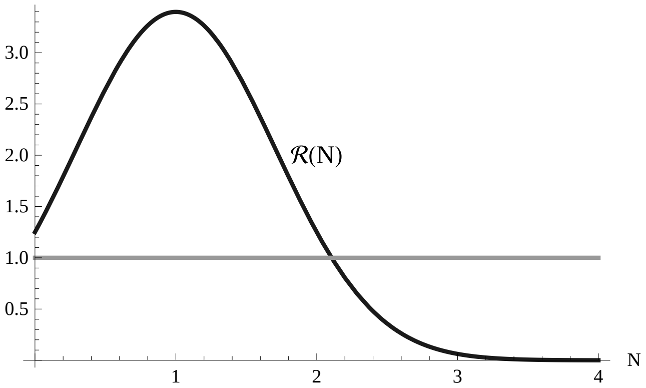

Figure 3. Allee effect in the case when $R_0 > 1$. The equation $\mathcal{R}(N) = 1$ has a unique solution.

Case 1: Suppose $\mu(x, N)$ does not depend on N and we assume specific values for μ_0 and m. In particular, let $\mu_0(N) = 0$, $m(N) = 1$. Then, by Assumption 3.1 the net reproduction rate of the prey population takes the form

$$\mathcal{R}(N) = R_0\frac{\beta_0(N)}{\beta_0(0)} \tag{3.10}$$

We will assume a particular form of the function $\beta_0(N)$, or more precisely, a particular form of the net reproduction rate, and then we will show that there exists N^* such that $\mathcal{R}(N^*) = 1$. We consider the following specific form of the net reproduction rate:

$$\mathcal{R}(N) = R_0\frac{e^{-(N-a)^2}}{e^{-a^2}} = R_0e^{a^2-(N-a)^2} \tag{3.11}$$

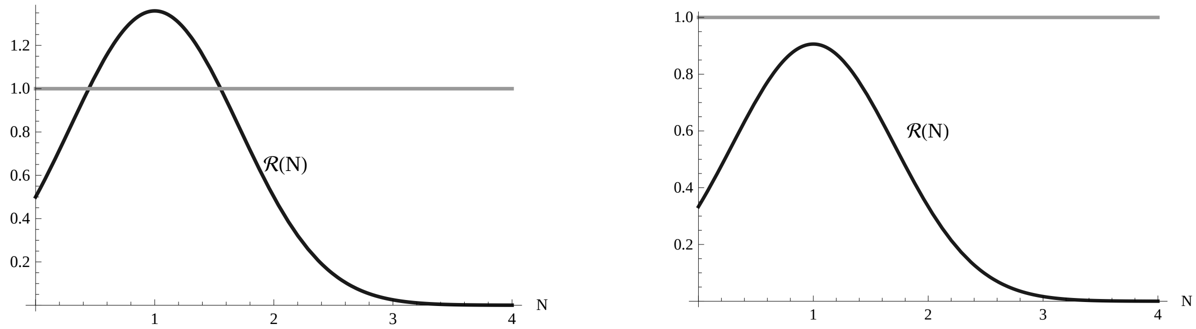

Figure 4. *Allee effect in the case $R_0 < 1$. Equation $\mathcal{R}(N) = 1$ can have two solutions (illustrated in the left figure) or no solutions (illustrated in the right figure).*

where a is a positive parameter. The example of a net reproduction rate in (3.11) is one of the simplest functions that can exhibit Allee effect. As Figure 3 shows the function increases for small values of the prey population size, that is when $N < a$, suggesting that the increase in prey population size benefits mating. The net reproductive rate decreases for large prey population sizes, suggesting that competition for resources takes precedence and hampers reproduction. Since $\mathcal{R}'(N) = R_0 e^{a^2-(N-a)^2}(-2(N-a))$, the derivative $R'(N) = 0$ at $N = a$ only. Also we observe that $N = a$ is a local maximum for the graph and $R(N) \to 0$ as $N \to \infty$. We consider two cases

(1) **If $R_0 > 1$.** In this case there exists only one N^* such that $R(N^*) = 1$. Figure 3 illustrates this scenario.
(2) **If $R_0 < 1$.** In this case the graph either does not cross the line $y = 1$ or crosses twice. Thus, there exist either 0 or two N^* such that $R(N^*) = 1$. The graph in Figure 4 shows that.

In the case $R_0 < 1$ the critical value of the parameter a such that the equation $\mathcal{R}(N) = 1$ transitions from having two solutions to having no solutions is denoted by a_{cr}. This critical value occurs when, through manipulations on a, the graph of $\mathcal{R}(N) = R_0 e^{a^2-(N-a)^2}$ touches the line $y = 1$. In this case we have that $\mathcal{R}'(N) = 0$ at $N = a$. Hence the critical value of $a = a_{cr}$ is given by the solution of the following equation

$$\mathcal{R}(N^*_{cr}, a_{cr}) = 1. \tag{3.12}$$

Thus, the critical value of the parameter a is

$$a_{cr} = \sqrt{\ln \frac{1}{R_0}}. \tag{3.13}$$

The corresponding value of N^* obtained when $a = a_{cr}$ is N^*_{cr} and it is a double root of the equation $\mathcal{R}(N) = 1$. All other roots of the equation $\mathcal{R}(N) = 1$, when $a \neq a_{cr}$ are simple roots. We note that $R_0 < 1$, we have $\frac{1}{R_0} > 1$ and the square root is well defined and positive. The equilibria that are obtained in the case $R_0 < 1$ are called *subthreshold equilibria.*

The above example can be extended to allow for more than two equilibria. For instance, assume $a < b$ are two distinct parameters. Consider the following specific function

$$\mathcal{R}(N) = R_0 e^{-(N-a)^2(N-b)^2+a^2b^2}.$$

We have again that $\mathcal{R}(0) = R_0$. It can be seen that $\mathcal{R}'(N) = 0$ at $N = a, b, \frac{a+b}{2}$. Therefore, the curve has only 3 horizontal tangent lines and hence it bends three times. Also as $N \to \infty$ we have $\mathcal{R}(N) \to 0$. Consequently, if $\mathcal{R}(0) > 1$ there exists either one or three N^* such that $\mathcal{R}(N^*) = 1$. If $\mathcal{R}(0) < 1$, the equation $\mathcal{R}(N) = 1$ may have no solutions, two solutions or four solutions, if all solutions are simple. We illustrate this last case in Figure 5. We conclude that even in the case when the mortality rate does not depend on N, we may have multiple super and subthreshold equilibria.

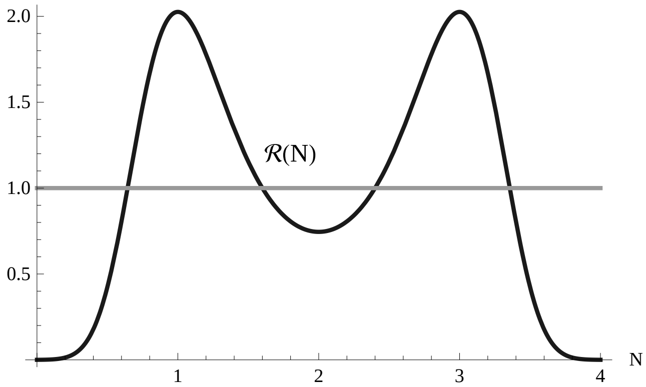

FIGURE 5. Multiple subthreshold equilibria. We have $\mathcal{R}(0) < 1$.

Case 2: In this case we, in fact, consider the general case where both the birth rate and the death rate may depend on N. We recall that the general net reproduction rate defined as a function of the total prey size is given by (3.8). Equilibria of the total prey population size are solutions of the equation $\mathcal{R}(N) = 1$. We define in analogy with the example above, the *intrinsic reproduction number of the prey population* as

$$\mathcal{R}_0 = \mathcal{R}(0) = \int_0^\infty \frac{\beta(x,0)}{g(x)} e^{-\int_0^x \frac{\mu(x,0)}{g(s)} ds} dx. \tag{3.14}$$

The assumptions on the birth rate and death rate as functions of N (Assumptions 2.1) guarantee that

$$\lim_{N\to\infty} \mathcal{R}(N) = 0$$

which states that the net reproduction rate of the prey population approaches zero as the prey population size grows to infinity. Thus, in the case when $\mathcal{R}_0 > 1$, that is $\mathcal{R}(0) > 1$ the equation $\mathcal{R}(N) = 1$ has at least one positive solution N^*. In the case $\mathcal{R}_0 < 1$, as the examples above suggest, the equation $\mathcal{R}(N) = 1$ may or may not have solutions. We summarize the findings in the following Theorem.

Theorem 3.1. *We consider the following two cases:*

(1) *Let* $\mathcal{R}_0 > 1$. *Then, there is at least one positive prey-only equilibrium* $\mathcal{E}_1 = (u_1(0), 0, N_1^*)$. *If there are multiple solutions to the equation* $\mathcal{R}(N) = 1$ *and they are all simple, then there is an odd number of them* $N_1^* \dots N_k^*$ *where* k *is odd. Each of these solutions gives a prey-only equilibrium* $\mathcal{E}_j = (u_j(0), 0, N_j^*)$ *for* $j = 1, \dots, k$.
(2) *Let* $\mathcal{R}_0 < 1$. *Then, there may be no positive prey-only equilibrium. If there are multiple solutions to the equation* $\mathcal{R}(N) = 1$ *and they are all simple, then there is an even number of them* $N_1^* \dots N_k^*$ *where* k *is even. Each of these solutions gives a prey-only equilibrium* $\mathcal{E}_j = (u_j(0), 0, N_j^*)$ *for* $j = 1, \dots, k$.

We note that the requirement that *all* equilibria are simple is very important. The general case when some equilibria can have higher multiplicities is much more complex. However, this condition can fail, and some solutions of $\mathcal{R}(N) = 1$ can have higher multiplicity. In this case the parameters of the model have to satisfy additional constrains. Consequently, for very few choices of the parameters, equilibria of higher multiplicity are possible. In the example in Case 1, the parameter value for which the root N^* has a higher multiplicity, is only a_{cr}.

3.2. **Predator-prey coexistence equilibria.**

In this case we are looking for equilibria $(u(0), P^*, N^*)$ where $P^* \neq 0$.

Assumption 3.2. *Assume*

(1) *The reproduction number of the prey population in the absence of the predator satisfies:* $\mathcal{R}_0 > 1$.
(2) *The equation* $\mathcal{R}(N) = 1$ *has* k *solutions* $N_1^*, \dots N_k^*$, *where* k *is odd. We assume that all solutions are simple.*

We define the *predator reproduction number at the* N_j *prey-only equilibrium*

$$\mathcal{R}_{p,j} = \frac{N_j^* \displaystyle\int_0^\infty \alpha(x)\gamma(x)\pi(x, 0, N_j^*)}{d \displaystyle\int_0^\infty \pi(x, 0, N_j^*)dx}. \tag{3.15}$$

The predator's reproduction number gives the ability of the predator to invade the N_j^* equilibrium of the prey. In particular, if $\mathcal{R}_{p,j} > 1$, then the predator can invade the jth prey-only equilibrium.

Assumption 3.3. *Assume that there exists* $N_j^* > 0$ *such that:*

(1) *The predator's reproduction number at the previous prey-only equilibrium* $\mathcal{R}_{p,j-1} < 1$, *that is the predator cannot invade the* N_{j-1}^**th prey-only equilibrium;*
(2) *The predator's reproduction number* $\mathcal{R}_{p,j} > 1$, *that is, we assume that the predator can invade the* j*th prey-only equilibrium.*
(3) *Assume also,* j *is odd.*

We note that if $\mathcal{R}_{p,1} > 1$, then the above assumption would be trivially satisfied.

In the case of predator-prey coexistence equilibria, the non-linear system for the equilibria (3.5) does not decouple. From the second equation we may express $u(0)$ and eliminate it from the system. We have:

$$u(0)g(0) = \frac{d}{\int_0^\infty \frac{\alpha(x)\gamma(x)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{P\gamma(s)}{g(s)}ds} dx}. \tag{3.16}$$

Replacing $u(0)g(0)$ in the equation for the total prey population size we obtain the following equation in P and N:

$$N = \frac{\int_0^\infty \frac{d}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{P\gamma(s)}{g(s)}ds} dx}{\int_0^\infty \frac{\alpha(x)\gamma(x)}{g(x)} e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{P\gamma(s)}{g(s)}ds} dx}.$$

This equation coupled with the renewal equation leads to the following non-linear system for the variables N and P.

$$\begin{aligned} &\int_0^\infty \beta(x,N)\pi(x,P,N)dx = 1, \\ &N = \frac{\displaystyle\int_0^\infty d\pi(x,P,N)dx}{\displaystyle\int_0^\infty \alpha(x)\gamma(x)\pi(x,P,N)dx}. \end{aligned} \tag{3.17}$$

This is a non-linear system in N, P. It does not decouple. We are looking for conditions that give a non-zero positive solution of that system. Each positive solution of the system (3.17) gives one coexistence equilibrium $\mathcal{E}^* = (u^*(0), P^*, N^*)$. The first equation in system (3.17) prompts us to define the net reproduction rate of the prey in the presence of the predator. Denote the *net reproduction rate of the prey in the presence of the predator* by

$$\mathcal{R}(N,P) = \int_0^\infty \beta(x,N)\pi(x,P,N)dx. \tag{3.18}$$

The first equation in system (3.17) gives $\mathcal{R}(N,P) = 1$. We use the implicit function theorem to solve for P as a function of N. For each arbitrary but fixed N, the equation

$$\mathcal{R}(N,P) = 1$$

as an equation of P only has a unique solution, which, however, may be positive or negative. This defines $P = f(N)$ as a continuous function for all $N \geq 0$. Moreover,

$$\frac{\partial \mathcal{R}(N, f(N))}{\partial P} = -\int_0^\infty \beta(x,N)\left(\int_0^x \frac{\gamma(s)}{g(s)}ds\right)\pi(x, f(N), N)dx < 0$$

since $\gamma(x) > 0$ on a set of positive measure. The function $P = f(N)$ has the following properties:

- $f(N_j^*) = 0$, that is the predator equilibrium size at the prey-only equilibria is zero.

- Since all prey-only equilibria are simple, $f(N)$ has an alternating sign in the consecutive intervals. Since, $\mathcal{R}_0 > 1$ the signs are the following

$$\begin{cases} \text{f(N)}> 0 & \text{on} \quad (0, N_1^*) \\ \text{f(N)}< 0 & \text{on} \quad (N_1^*, N_2^*) \\ \dots & \\ \text{f(N)}> 0 & \text{on} \quad (N_{k-1}^*, N_k^*) \end{cases} \tag{3.19}$$

Now we replace $P = f(N)$ in the second equation of (3.17). After replacing P the second equation in (3.17), we obtain an equation in N only. We can rearrange the terms in that equation to get the following form.

$$\int_0^\infty (N\alpha(x)\gamma(x) - d)\frac{1}{g(x)}e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{f(N)\gamma(s)}{g(s)}ds}dx = 0 \tag{3.20}$$

We recall that we assume that there exists a prey-only equilibrium, N_j^* such that the predator can invade this equilibrium, that is $\mathcal{R}_{p,j} > 1$. We introduce the following notation. Let the left hand side of the equation (3.20) be denoted by $F(N)$:

$$F(N) := \int_0^\infty (N\alpha(x)\gamma(x) - d)\frac{1}{g(x)}e^{-\int_0^x \frac{\mu(x,N)}{g(s)}ds - \int_0^x \frac{f(N)\gamma(s)}{g(s)}ds}dx. \tag{3.21}$$

Clearly we can see that $F(0) < 0$. Thus, if $\mathcal{R}_{p,1} > 1$, we have $F(N_1^*) > 0$. Therefore, there exists $\hat{N} \in (0, N_1^*)$ such that $F(\hat{N}) = 0$. Then, the corresponding value of the predator population size is given by $\hat{P} = f(\hat{N})$, and since $\mathcal{R}_0 > 1$, this value of the predator size is positive.

In the general case since $\mathcal{R}_{p,j-1} < 1$, that implies that $F(N_{j-1}^*) < 0$. On the other hand, since, $\mathcal{R}_{p,j} > 1$, we have $F(N_j^*) > 0$. Therefore, there exist an $\hat{N} \in (N_{j-1}^*, N_j^*)$ such that $F(\hat{N}) = 0$. At the same time we have that $\hat{P} = F(\hat{N})$ and $\hat{P} > 0$. One can express the corresponding $\hat{u}(0)$ from equation (3.16). We summarize the findings in the following theorem.

Theorem 3.2. *Let Assumption 3.2 and Assumption 3.3 hold. Then there is at least one coexistence equilibrium of the predator and the prey* $\mathcal{E}^* = (\hat{u}(0), \hat{P}, \hat{N})$.

Several remarks are in order.

- Conditions in Assumption 3.2 and Assumption 3.3 are sufficient conditions for a coexistence equilibrium to exist. A coexistence equilibrium may exist if one or more conditions fail. For instance, even if prey's intrinsic reproduction number $\mathcal{R}_0 < 1$, coexistence may still occur.
- In the size-structured case, unlike ODE case, the coexistence equilibrium may not be unique. Intuitively, that may be the case since size-specific predation may affect some (say more abundant) sizes of a prey-only equilibrium, and lead to coexistence. Since more than one prey-only equilibrium exists, each of them can be potentially perturbed this way to a coexistence equilibrium, leading to multiple coexistence equilibria.

4. STABILITY ANALYSIS

In this section we consider the local stability of the solutions of the model (2.4) around an equilibrium point. We linearize the model around a general equilibrium $\mathcal{E} = (u(0), P^*, N^*)$ where $u(0)$ corresponds to $u^*(x) = u(0)g(0)\pi(x, P^*, N^*)$. We introduce the following perturbations

$$\begin{aligned} u(x,t) &= u^*(x) + \xi(x,t), \\ P(t) &= P^* + \eta(t), \\ N(t) &= N^* + n(t). \end{aligned} \tag{4.1}$$

The last equality holds since

$$N(t) = \int_0^\infty u(x,t)dx = \int_0^\infty (u^*(x) + \xi(x,t))dx = N^* + n(t).$$

It is clear from the above computations that

$$n(t) = \int_0^\infty \xi(x,t)dx \tag{4.2}$$

Since the birth rate $\beta(x, N)$ and the death rate $\mu(x, N)$ are non-linear functions of the total population size, we expand them around the equilibrium point as

$$\begin{aligned} \beta(x,N) &= \beta(x, N^* + n(t)) \\ &\qquad = \beta(x, N^*) + n(t)\beta'(x, N^*) + h.o.t \\ \mu(x,N) &= \mu(x, N^* + n(t)) \\ &\qquad = \mu(x, N^*) + n(t)\mu'(x, N^*) + h.o.t \end{aligned}$$

where, 'h.o.t' in the equation above represents the higher order terms i.e the terms that involve products of perturbations. Since we consider the local stability around the equilibrium point we neglect the higher order terms. Hence the linearized equations of the model (2.4) reduce to the following system:

$$\begin{aligned} &\xi_t + (g(x)\xi(x,t))_x = -\mu(x,N^*)\xi - \mu'(x,N^*)u^*(x)n(t) - \gamma(x)P^*\xi - \gamma(x)u^*(x)\eta, \\ &g(0)\xi(0,t) = \int_0^\infty \beta(x,N^*)\xi(x,t)dx + n(t)\int_0^\infty \beta'(x,N^*)u^*(x)dx, \\ &\eta' = P^*\int_0^\infty \alpha(x)\gamma(x)\xi(x,t)dx + \eta\int_0^\infty \alpha(x)\gamma(x)u^*(x)dx - d\eta, \end{aligned} \tag{4.3}$$

where $n(t)$ is given by (4.2). We use the linearizations above to investigate the stability of each type of equilibria: extinction, prey-only, and coexistence equilibria.

4.1. **Extinction equilibrium** $(u = 0, P = 0)$**.** Here we consider the equilibrium where there is no predator or prey in the model. We disturb the extinction equilibrium with a small value and then observe the behavior in the long run. The system for the perturbations above takes the form

$$\begin{aligned}
&\xi_t + (g(x)\xi(x,t))_x = -\mu_0(x)\xi(x,t),\\
&g(0)\xi(0,t) = \int_0^\infty \beta_0(x)\xi(x,t)dx,\\
&\eta' = -d\eta,
\end{aligned} \tag{4.4}$$

where we have used the following notation: $\beta_0(x) = \beta(x,0)$ and $\mu_0(x) = \mu(x,0)$.

To find the stability of the equilibrium point we investigate the eigenvalues of the linearized operator by setting $\xi(x,t) = e^{\lambda t}\overline{\xi}(x)$ and $\eta(t) = e^{\lambda t}\overline{\eta}$. Hence we have the following eigenvalue problem for the stability of the extinction equilibrium:

$$\begin{aligned}
&\lambda\overline{\xi}(x) + (g(x)\overline{\xi}(x))_x = -\mu_0(x)\overline{\xi}(x),\\
&g(0)\overline{\xi}(0) = \int_0^\infty \beta_0(x)\overline{\xi}(x)dx,\\
&\lambda\overline{\eta} = -d\overline{\eta}.
\end{aligned} \tag{4.5}$$

Clearly, $\lambda = -d$ is one of the eigenvalues which is negative. Further, we assume $\lambda \neq -d$ so that $\overline{\eta} = 0$. To find the remaining eigenvalues we look for nonzero solution of the first two equations. In particular, we solve the first equation:

$$\overline{\xi}(x) = \frac{g(0)\overline{\xi}(0)}{g(x)} e^{-\int_0^x \frac{\mu_0(\sigma)+\lambda}{g(\sigma)}d\sigma} \tag{4.6}$$

and replace it in the second equation, obtaining the following *characteristics equation*

$$\int_0^\infty \frac{\beta_0(x)}{g(x)} e^{-\int_0^x \frac{\mu_0(\sigma)+\lambda}{g(\sigma)}d\sigma} dx = 1. \tag{4.7}$$

We denote by

$$G(\lambda) = \int_0^\infty \frac{\beta_0(x)}{g(x)} e^{-\int_0^x \frac{\mu_0(\sigma)+\lambda}{g(\sigma)}d\sigma}.$$

Hence, the characteristic equation becomes $G(\lambda) = 1$. For λ real, $G(\lambda)$ is decreasing. Furthermore, it is clear from the definition of $G(\lambda)$ that as $\lambda \to \infty, G(\lambda) \to 0$. Furthermore,

$$G(0) = \mathcal{R}_0.$$

We have the following two cases:

(1) **If $\mathcal{R}_0 > 1$:** In this case $G(0) > 1$. Therefore, then there exists positive real solution $\lambda^* > 0$ to the equation $G(\lambda) = 1$. Hence, the extinction equilibrium is unstable.

(2) **If $\mathcal{R}_0 < 1$:** In this case $G(0) < 1$, then because of the monotonicity of $G(\lambda)$, the equation $G(\lambda) = 1$ has a unique real solution $\lambda^* < 0$. We now show that all other solutions to the characteristic equation $G(\lambda) = 1$, which are complex, have negative real part. Indeed, for λ complex with $\Re\lambda \geq 0$ we have

$$|G(\lambda)| \leq G(\Re\lambda) \leq \mathcal{R}_0 < 1.$$

Hence, there do not exist any non-negative real solutions, or solutions with non-negative real part of λ for the characteristic equation $G(\lambda) = 1$. We may conclude that the extinction equilibrium is locally asymptotically stable.

We summarize these findings in the following Theorem.

Theorem 4.1. *If the intrinsic reproduction number of the prey population* $\mathcal{R}_0 < 1$*, then the extinction equilibrium* $\mathcal{E}_0 = (0,0,0)$ *is locally asymptotically stable. If the intrinsic reproduction number of the prey* $\mathcal{R}_0 > 1$*, then the extinction equilibrium is unstable.*

We note that we cannot establish global stability of the extinction equilibrium in the case $\mathcal{R}_0 < 1$ because of the presence of subthreshold equilibria (see Figure 4).

4.2. **Prey-only equilibria.** The equilibria in this case are given by $\mathcal{E}_j = (u_j^*(x), 0, N_j^*)$ where $N_j^* = \int_0^\infty u_j^*(x)dx$. For arbitrary prey-only equilibrium $\mathcal{E} = (u^*(x), 0, N^*)$ the linearization of the original size-structured model (2.4) is obtained from the linearized system (4.3).

$$\begin{aligned} &\xi_t + (g(x)\xi(x,t))_x = -\mu(x,N^*)\xi(x,t) - \mu'(x,N^*)u^*n(t), \\ &g(0)\xi(x,t) = \int_0^\infty (\beta(x,N^*)\xi(x,t) + \beta'(x,N^*)u^*n(t))dx, \\ &\eta'(t) = \eta(t)\int_0^\infty \alpha(x)\gamma(x)u^*dx - d\eta, \end{aligned} \tag{4.8}$$

where $u^*(x)$ if given by (3.7). We can integrate the last equation in this system to obtain

$$\eta(t) = \eta_0 e^{(A_p - d)t} \tag{4.9}$$

where $A_p = \int_0^\infty \alpha(x)\gamma(x)u^*(x)dx$. We recall that for the jth prey-only equilibrium the predator invasion number is given by

$$\mathcal{R}_{p,j} = \frac{N_j^* \displaystyle\int_0^\infty \alpha(x)\gamma(x)\pi(x,0,N_j^*)dx}{d\displaystyle\int_0^\infty \pi(x,0,N_j^*)dx}.$$

We note that the definition for A_p and formula for $u(0)$ given by (3.16) imply that $\mathcal{R}_{p,j} = A_p/d$. Therefore, if the predator can invade the prey-only equilibrium $\mathcal{R}_{p,j} > 1$, then $A_p > d$, and the jth prey-only equilibrium is unstable. We summarize that in following theorem.

Theorem 4.2. *The* j*th prey-only equilibrium* $\mathcal{E}_j = (u_j(0), 0, N_j^*)$ *is unstable if* $\mathcal{R}_{p,j} > 1$.

Proof. If $\mathcal{R}_{p,j} > 1$ then that implies $A_p > d$ and as a result from the solution $\eta(t)$ given in equation (4.9) we have that $\eta(t) \to \infty$ as $t \to \infty$. Hence the equilibrium is unstable. ☐

In the remainder of this section we consider prey-only equilibria $\mathcal{E}_j$ that cannot be invaded by the predator, that is $\mathcal{R}_{p,j} < 1$. We will again drop the subscript j. To obtain the eigenvalue problem for the linearized operator, we are looking for a solution of (4.8) that has the form $\xi(x,t) = e^{\lambda t}z(x)$ and $\eta(t) = \eta e^{\lambda t}$. From the definition of $n(t)$ we can get that

$$n(t) = \int_0^\infty \xi(x,t)dx = e^{\lambda t}\int_0^\infty z(x)dx = n_0 e^{\lambda t}.$$

If we substitute the above quantities in the equations (4.8) then we can obtain the following eigenvalue problem:

$$\begin{aligned}
&\lambda z(x) + (g(x)z(x))_x = -\mu(x,N^*)z(x) - \mu'(x,N^*)n_0u^*(x) - \gamma(x)\eta u^*(x),\\
&g(0)z(0) = \int_0^\infty \beta(x,N^*)z(x)dx + n_0\int_0^\infty \beta'(x,N^*)u^*dx,\\
&\eta\lambda = \eta A_p - \eta d.
\end{aligned} \tag{4.10}$$

In the above system we are looking for a non-trivial solution $(z(x),\eta)$.
Option 1: Let $\lambda = A_p - d$. Then $\lambda < 0$. Furthermore, the last equation is satisfied for every η where $\eta \neq 0$. We may choose as a non zero solution of equations (4.10) $(z(x),\eta)$, where $z(x)$ is the solution of the first two equations with the given, chosen η. Such a solution $z(x)$ exists if $\lambda = A_p - d$ is not an eigenvalue of the first two equations of the system (4.10) with $\eta = 0$.
Option 2: $\lambda \neq A_p - d$. We need to have $\eta = 0$. Then $\lambda\eta = (A_p - d)\eta$. We may have a non-zero eigenvector, if the remaining two equations have a non-zero solution $z(x)$. The remaining eigenvalues are solutions of the following system.

$$\lambda z(x) + (g(x)z(x))_x = -\mu(x,N^*)z(x) - \mu'(x,N^*)u^*n_0, \tag{4.11}$$

$$g(0)z(0) = \int_0^\infty \beta(x,N^*)z(x)dx + n_0\int_0^\infty \beta'(x,N^*)u^*dx. \tag{4.12}$$

Here $z(x)$ can be positive or negative. We call $\omega(x) = \mu'(x,N^*)u^*n_0$.
Subcase 1: Here we assume $\mu(x,N) = \mu(x)$ that is μ does not depend on N so that we have $\mu'(x,N^*) = 0$ and as a result $\omega(x) = 0$. This reduces the system to the following set of equations.

$$\lambda z(x) + (g(x)z(x))_x = -\mu(x)z(x), \tag{4.13}$$

$$g(0)z(0) = \int_0^\infty \beta(x,N^*)z(x)dx + n_0\int_0^\infty \beta'(x,N^*)u^*dx, \tag{4.14}$$

which can be easily solved to obtain $g(x)z(x) = g(0)z(0)e^{-\int_0^\infty \frac{\lambda+\mu(s)}{g(s)}ds}$. Substituting this in the second equation above we have the following characteristic equation

$$1 = \int_0^\infty \frac{\beta(x,N^*)}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx + \int_0^\infty \beta'(x,N^*)u^*dx\int_0^\infty \frac{1}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx. \tag{4.15}$$

We define

$$G(\lambda) = \int_0^\infty \frac{\beta(x,N^*)}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx + F\int_0^\infty \frac{1}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx \tag{4.16}$$

where the constant F is given by

$$F = \int_0^\infty \beta'(x,N^*)u^*dx.$$

Furthermore, we denote by

$$\begin{aligned}
K(\lambda) &= \int_0^\infty \frac{\beta(x,N^*)}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx,\\
L(\lambda) &= \int_0^\infty \frac{1}{g(x)}e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)}ds}dx.
\end{aligned} \tag{4.17}$$

Hence, the function $G(\lambda)$ takes the form $G(\lambda) = K(\lambda) + FL(\lambda)$. Clearly for $\lambda = 0$ we have

$$G(0) = K(0) + FL(0) = \mathcal{R}(N^*) + FL(0) = 1 + FL(0) \tag{4.18}$$

since N^* is an equilibrium total population and is a solution to the equation $\mathcal{R}(N) = 1$. It is clear from the form of $G(\lambda)$ that for λ real, as $\lambda \to \infty$, $G(\lambda) \to 0$. Hence the characteristic equation $G(\lambda) = 1$ has a positive real solution if $G(0) > 1$. A positive real solution to the characteristics equation implies that the prey-only equilibrium $\mathcal{E}_j$ is unstable. Since $G(0) > 1$ if and only if $F > 0$, then $F > 0$ is a condition that implies instability of the system, even if $\lambda = A_p - d < 0$. We summarize this result in the following lemma.

Lemma 4.1. *Assume $\mu(x, N) = \mu(x)$. If $F > 0$, then the jth prey-only equilibrium $\mathcal{E}_j$ is unstable.*

Concerning stability of the prey-only equilibria we have the following lemma.

Lemma 4.2. *Assume $F < 0$, the birth rate $\beta(x, N) = \beta(N)$. Furthermore, assume that for the prey-only equilibrium with total population size N^* the following inequality holds:*

$$-F < 2\beta(N^*).$$

Then the characteristic equation $G(\lambda) = 1$ has only roots with negative real part.

Proof. We consider the characteristic equation $G(\lambda) = 1$, where $G(\lambda)$ is given by (4.16). The assumption that $F < 0$ implies that $G(0) < 1$. Assume there exists a root $\lambda = a+ib$ of $G(\lambda) = 1$ where $a \geq 0$. That implies $|(G(\lambda)| = 1$. We have

$$\begin{aligned} G(\lambda) &= \int_0^\infty \frac{\beta(N^*)}{g(x)} e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)} ds} dx + F \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)} ds} dx \\ &= (\beta(N^*) + F) \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)} ds} dx. \end{aligned}$$

Taking absolute values and using the fact that $G(\lambda) = 1$, we have

$$\begin{aligned} 1 = |G(\lambda)| &= |(\beta(N^*) + F) \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\lambda+\mu(s)}{g(s)} ds} dx| \\ &\leq |(\beta(N^*) + F)| \int_0^\infty \frac{1}{g(x)} e^{-\int_0^x \frac{\Re(\lambda)+\mu(s)}{g(s)} ds} dx \\ &< \int_0^\infty \frac{1}{g(x)} \beta(N^*) e^{-\int_0^x \frac{\mu(s)}{g(s)} ds} dx = 1. \end{aligned}$$

We note that our assumption on $-F < 2\beta(N^*)$ implies that we have $|\beta(N^*) + F| < |\beta(N^*)| = \beta(N^*)$. The last sequence of inequalities leads to $1 < 1$ which is a contradiction.

Thus there cannot exists a root λ which has a non-negative real part when $G(0) < 1$. Thus, our claim is proved. □

A couple of remarks are in order.

- The condition on the sign of F is related to the net reproduction rate $\mathcal{R}(N)$. In particular, in the case when μ is not a function of N, the rate of change of the prey population net reproduction rate at the equilibrial total prey population size N^* is given by
$$\mathcal{R}'(N^*) = \int_0^\infty \frac{\beta'(x,N^*)}{g(x)} e^{-\int_0^x \frac{\mu(s)}{g(s)}ds} dx.$$
Hence, $F = u(0)g(0)\mathcal{R}'(N^*)$, that is F has the sign of the rate of change of the net reproductive rate at the prey-only equilibrium. So we established that if the net reproduction rate is increasing at the equilibrium, the equilibrium is unstable. If the net reproduction rate is decreasing, the equilibrium may be stable subject to additional assumptions.
- As we show below, if μ is constant, and $F < 0$, equilibrium is locally asymptotically stable with a general birth rate $\beta(x,N)$.
- In the case when $F < 0$, if the birth and the death rate depend on x, then oscillations may be possible.

Subcase 2: Now we assume $\mu(x,N) = \mu(N)$, that is, μ depends on N only. Further, assume that $\mu'(N) \geq 0$. System (4.11)-(4.12) takes the form

$$\begin{aligned} \lambda z(x) + (g(x)z(x))_x &= -\mu(N^*)z(x) - \mu'(N^*)u^* n_0, \\ g(0)z(0) &= \int_0^\infty \beta(x,N^*)z(x)dx + n_0 \int_0^\infty \beta'(x,N^*)u^* dx. \end{aligned} \tag{4.19}$$

We recall that $u^*(x) = \frac{u(0)g(0)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)}{g(s)}ds}$. We solve the differential equation for $z(x)$ treating n_0 as given to obtain

$$z(x) = \frac{g(0)z(0)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(s)}ds} - \frac{\mu'(N^*)u(0)g(0)n_0}{\lambda} \left[\frac{e^{-\int_0^x \frac{\mu(N^*)}{g(s)}ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(s)}ds}}{g(x)} \right]. \tag{4.20}$$

From definition of $n_0 = \int_0^\infty z(x)dx$ and using the formula for $z(x)$ we can express n_0 in terms of $g(0)z(0)$:

$$n_0 = \frac{g(0)z(0)}{\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)}}. \tag{4.21}$$

We substitute $z(x)$ and n_0 back in the second equation of (4.19). We obtain the following characteristic equation:

$$\begin{align} 1 = \int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(s)}ds} dx \left[1 + \frac{\mu'(N^*)u(0)g(0)}{\lambda(\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)})} \right] \tag{4.22} \\ - \frac{\mu'(N^*)u(0)g(0)}{\lambda(\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)})} + \frac{F}{\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)}} \tag{4.23} \end{align}$$

where $F = \int_0^\infty \beta'(x,N^*)u^*(x)dx$. Denoting by $G(\lambda)$ the expression on the right hand side of the above equation, we can write the characteristic equation as $G(\lambda) = 1$. The eigenvalues of the system (4.19) are the real and complex solutions of that equation. As before, it can be seen that for λ real $G(\lambda) \to 0$ as $\lambda \to \infty$. $G(0)$ is defined as the limit of the function $G(\lambda)$ as $\lambda \to 0$. Hence,

$$\begin{aligned} G(0) = 1 &+ \frac{F}{\mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)}} \\ &- \frac{\mu'(N^*)u(0)g(0)}{(\mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)})} \int_0^\infty \frac{\beta(x,N^*)}{g(x)} \left(\int_0^x \frac{1}{g(s)} ds\right) e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} dx. \end{aligned}$$

The relationship of $G(0)$ with one is determined by the sign of the expression $F - \mu'(N^*)g(0)u(0) \int_0^\infty \beta(x,N^*) e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} (\int_0^x \frac{ds}{g(s)}) dx$. We have that $G(0) > 1$ if and only if

$$F - \mu'(N^*)g(0)u(0) \int_0^\infty \beta(x,N^*) e^{-\int_0^x \frac{\mu(N^*)}{g(s)} ds} \left(\int_0^x \frac{ds}{g(s)}\right) dx > 0. \tag{4.24}$$

In this case by a similar argument as before we can say that the equilibrium is unstable. We now show that the sign of the expression above is determined by the rate of change of the net reproduction rate at the equilibrium total prey population size N^*. In particular, we have

$$\begin{aligned} \mathcal{R}'(N^*) = &\int_0^\infty \beta'(x,N^*) e^{-\mu(N^*) \int_0^x \frac{1}{g(s)ds}} dx \\ &- \mu'(N^*) \int_0^\infty \frac{\beta(x,N^*)}{g(x)} \left(\int_0^x \frac{1}{g(s)} ds\right) e^{-\mu(N^*) \int_0^x \frac{1}{g(s)ds}} dx. \end{aligned}$$

Thus, we find again that if the net reproduction rate of the prey population is increasing through the equilibrium, the prey-only equilibrium is unstable. We summarize that in the following lemma:

Lemma 4.3. *Assume $\mu(x,N) = \mu(N)$ and $\mu'(N) \geq 0$. If $\mathcal{R}'(N_j^*) > 0$, then the prey-only equilibrium $\mathcal{E}_j$ is unstable.*

Stability of an equilibrium in this case is given by the following lemma.

Lemma 4.4. *Assume $\mu(x,N) = \mu(N)$ and $\mu'(N) \geq 0$. If $F < 0$ there cannot exist any root λ of the characteristic equation $G(\lambda) = 1$ with $\Re(\lambda) \geq 0$.*

Proof. Assume $\Re(\lambda) \geq 0$. We rewrite the characteristics equation $G(\lambda) = 1$ in the following form.

$$\begin{aligned} &\left[1 + \frac{\mu'(N^*)u(0)g(0)}{\lambda(\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)})}\right] = \\ &= \int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(s)} ds} dx \left[1 + \frac{\mu'(N^*)u(0)g(0)}{\lambda(\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)})}\right] \\ &+ \frac{F}{\lambda + \mu(N^*) + \frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)}}. \end{aligned} \tag{4.25}$$

Simplifying the expression we have

$$\int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\mu(N^*)+\lambda}{g(s)}ds} dx = 1 - \frac{F\lambda}{\lambda(\lambda+\mu(N^*)+\frac{\mu'(N^*)g(0)u(0)}{\mu(N^*)}) + \mu'(N)g(0)u(0)}. \tag{4.26}$$

The absolute value of left side of the previous equation is less or equal to one. We can show that the absolute value of right side of the equation is greater than one. We can treat the right side of the equation as $1 + \frac{k\lambda}{\lambda^2+r\lambda+s}$. It can be shown that the real part of this expression is strictly greater than one. Hence absolute value is greater than one, which leads to a contradiction. This shows that there do not exist any roots with non-negative real part for the characteristic equation $G(\lambda) = 1$ when F is negative. ☐

4.3. **Stability of a coexistence equilibrium.** The equilibrium in this case is represented by $(u^*(x), P^*, N^*)$, where $N^* = \int_0^\infty u^*(x)dx$. We will investigate the local stability of the coexistence equilibrium starting from the linearized system (4.3). First we notice that from the equation for the equilibrium we have

$$\int_0^\infty \alpha(x)\gamma(x)u^*(x)dx = d.$$

That simplifies the third equation in (4.3). We are looking for a solution of the form $\xi(x,t) = e^{\lambda t}\xi(x), \eta(t) = \eta e^{\lambda t}, n(t) = ne^{\lambda t}$. We substitute this form of solution into equations (4.3) to get,

$$\begin{aligned} (g(x)\xi(x))_x &= -\lambda\xi(x) - \mu\xi(x) - \mu' u^*(x)n - \gamma(x)P^*\xi(x) - \gamma(x)u^*\eta, \\ g(0)\xi(0) &= \int_0^\infty \beta(x,N^*)\xi(x)dx + n\int_0^\infty \beta'(x,N^*)u^*dx, \\ \lambda\eta &= P^*\int_0^\infty \alpha(x)\gamma(x)\xi(x)dx, \end{aligned} \tag{4.27}$$

where

$$n = \int_0^\infty \xi(x)dx.$$

In what follows in this subsection we consider two cases: constant predation and size-specific predation.

Case 1: Constant predation: We make the following simplifying assumptions

Assumption 4.1. *Assume*

1. *μ is a function of N^* only, that is, $\mu(x,N^*) = \mu(N^*)$;*
2. *$\gamma(x)$ is constant: $\gamma(x) = \gamma$;*
3. *$\alpha(x)$ is constant: $\alpha(x) = \alpha$.*

In the previous section we showed that with the above assumption on μ, and any function β, the prey-only equilibrium is locally asymptotically stable. In this section we will see that, even if predation is constant with respect to size, it has the ability to destabilize the predator-prey coexistence equilibrium.

With the above assumptions, from equations (4.27) we have:

$$
\begin{aligned}
(g(x)\xi(x))_x + \left(\frac{\lambda+\mu+\gamma P^*}{g(x)}\right) g(x)\xi(x) &= -(\mu'(N)n+\gamma\eta)u^*(x), \\
g(0)\xi(0) &= \int_0^\infty \beta(x,N^*)\xi(x)dx + Fn, \\
\lambda &= \frac{P^*\alpha\gamma n}{\eta}.
\end{aligned}
\tag{4.28}
$$

Integrating the first equation in the system above we obtain the following formula:

$$
g(x)\xi(x) = g(0)\xi(0)e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds} - u(0)g(0)(\mu' n+\gamma\eta)e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}\int_0^x \frac{e^{\int_0^s \frac{\lambda}{g(\sigma)}d\sigma}}{g(s)}ds.
\tag{4.29}
$$

Which leads to the following form of the equations

$$
\begin{aligned}
\xi(x) &= g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}}{g(x)} - \frac{u(0)g(0)(\mu' n+\gamma\eta)}{g(x)}e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}\frac{[e^{\int_0^x \frac{\lambda}{g(s)}ds}-1]}{\lambda} \\
&= g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}}{g(x)} - \frac{u(0)g(0)(\mu' n+\gamma\eta)}{\lambda}[\frac{e^{-\int_0^x \frac{\mu+\gamma P^*}{g(s)}ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}}{g(x)}]
\end{aligned}
$$

We know that $n = \int_0^\infty \xi(x)dx$. Integrating $\xi(x)$ we have

$$
n = \frac{g(0)\xi(0)}{\lambda+\mu+\gamma P^*} - \frac{u(0)g(0)(\mu' n+\gamma\eta)}{(\mu+\gamma P^*)(\lambda+\mu+\gamma P^*)}.
\tag{4.30}
$$

Solving for n from (4.30) we have

$$
n = \frac{g(0)\xi(0)\lambda}{\lambda^2+L\lambda+K}, \qquad \eta = \frac{g(0)\xi(0)P^*\alpha\gamma}{\lambda^2+L\lambda+K},
$$

where we have introduced the following notation:

$$
K = \frac{u(0)g(0)\gamma^2 P^*\alpha}{\mu+\gamma P^*}, \qquad L = \mu+\gamma P^* + \frac{u(0)g(0)\mu'}{\mu+\gamma P^*}.
$$

Substituting the value of η and n we have the following form of $\xi(x)$.

$$
\begin{aligned}
\xi(x) = {} & g(0)\xi(0)\frac{e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}}{g(x)} \\
& - \frac{u(0)g(0)g(0)\xi(0)}{(\lambda^2+\lambda L+K)}[\mu' + \frac{\gamma P^*\alpha\gamma}{\lambda}][\frac{e^{-\int_0^x \frac{\mu+\gamma P^*}{g(s)}ds}}{g(x)} - \frac{e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds}}{g(x)}]
\end{aligned}
\tag{4.31}
$$

Substituting this expression in the second equation of (4.28) we obtain the characteristic equation

$$
G(\lambda) = 1
$$

where we have the following form of $G(\lambda)$:

$$G(\lambda) = \int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds} dx \left[1 + \frac{u(0)g(0)}{\lambda^2+L\lambda+K}(\mu' + \frac{\gamma^2 P^* \alpha}{\lambda})\right] - \frac{u(0)g(0)}{\lambda^2+L\lambda+K}(\mu' + \frac{\gamma^2 P^*\alpha}{\lambda}) + \frac{F\lambda}{\lambda^2+L\lambda+K}. \tag{4.32}$$

We observe here that $G(0)$ has the following form:

$$G(0) = 1 - \frac{u(0)g(0)\gamma^2 P^*\alpha}{K} \int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\mu+\gamma P^*}{g(s)}ds} \int_0^x \frac{ds}{g(s)} dx. \tag{4.33}$$

This shows that we always have: $G(0) < 1$. We can rewrite the characteristic equation in the following form:

$$1 - \frac{F\lambda^2}{\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2 P^*\alpha u(0)g(0)} = \int_0^\infty \frac{\beta(x,N^*)}{g(x)} e^{-\int_0^x \frac{\lambda+\mu+\gamma P^*}{g(s)}ds} dx. \tag{4.34}$$

Stability of the coexistence equilibrium can be established in the following special case:

Lemma 4.5. *Let Assumptions 4.1 hold. Assume $F < 0$, and the size-specific birth rate has the form*

$$\beta(x,N^*) = \beta(N^*)e^{-\int_0^x \frac{\rho}{g(s)}ds}$$

where ρ is a given non-negative parameter. Then the predator-prey coexistence equilibrium is locally asymptotically stable.

Proof. The denominator of the left-hand side in the characteristic equation can be rewritten in the form:

$$\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2 P^*\alpha u(0)g(0) = (\lambda+\mu+\gamma P^*)[\lambda^2 + Q\lambda + R] \tag{4.35}$$

where

$$Q = \frac{u(0)g(0)\mu'}{\mu+\gamma P^*}, \qquad R = \frac{u(0)g(0)\gamma^2 P^*\alpha}{\mu+\gamma P^*}.$$

We rewrite the characteristic equation in the form

$$\frac{F\lambda^2}{\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2 P^*\alpha u(0)g(0)} = 1 - \frac{\beta(N^*)}{\lambda+\rho+\mu+\gamma P^*}.$$

The equations for the equilibrium imply

$$\rho + \mu + \gamma P^* = \beta(N^*).$$

Hence, the characteristic equation simplifies to

$$\frac{F\lambda}{\lambda^3 + L\lambda^2 + (K + u(0)g(0)\mu')\lambda + \gamma^2 P^*\alpha u(0)g(0)} = \frac{1}{\lambda+\rho+\mu+\gamma P^*}$$

which rewritten as a cubic equation becomes

$$\lambda^3 + \hat{A}\lambda^2 + \hat{B}\lambda + \hat{C} = 0$$

where the coefficients are given by

$$\hat{A} = Q + (\mu + \gamma P^*) - F \tag{4.36}$$

$$\hat{B} = (\mu + \gamma P^*)Q + R - F(\rho + \mu + \gamma P^*) \tag{4.37}$$

$$\hat{C} = (\mu + \gamma P^*)R \tag{4.38}$$

Since, $F < 0$, it follows that $\hat{A} > 0$, $\hat{B} > 0$, and $\hat{C} > 0$. Furthermore, it is not hard to see that $\hat{A}\hat{B} > \hat{C}$. Thus, Routh-Hurwitz criteria imply that the roots are negative or have negative real parts. Oscillations in this case do not occur. □

In the following theorem, we consider a special case where we show that oscillations may occur.

Theorem 4.3. *Assume $F < 0$, μ is a constant that does not depend on N^*, and the size-specific birth rate has the following form*

$$\beta(x, N^*) = \beta(N^*)\chi_{[A,\infty)}(x)$$

where $\chi_{[A,\infty)}$ is the characteristic function of the interval $[A, \infty)$, that is $\chi(x) = 1$, if $x > A$ and zero elsewhere. Assume further that the following inequality holds:

$$\frac{u(0)g(0)\gamma^2 P^* \alpha}{\mu + \gamma P^*} < 2(\mu + \gamma P^*)(-F). \tag{4.39}$$

Then, Hopf bifurcation occurs for some value of A, and the system exhibits sustained oscillations.

The proof is provided in the appendix. We note that inequality (4.39) can be rewritten in the form

$$\frac{1}{2}\frac{\gamma^2 P^* \alpha}{\mu + \gamma P^*} e^{(\mu+\gamma P^*)A} < -\beta'(N^*)$$

which can be obtained from writing F in terms of the parameters. This inequality implies that the oscillations occur if the predator size P^* at equilibrium and predator predation rate γP^* are sufficiently small relative to the growth rate of the prey at the equilibrium $-\beta'(N^*)$. In other words, for an equilibrium for which prey's net reproductive rate is decreasing ($\beta'(N^*) < 0$), predator's abundance should be low for oscillations to occur.

Case 2: Size-specific predation: We make the following simplifying assumptions

ASSUMPTION 4.2. *Assume*

1. *$\mu(x, N^*) = \mu$ is a constant;*
2. *$\gamma(x)$ is given by*

$$\gamma(x) = \begin{cases} 0 & 0 \le x < A \\ \gamma & x > A \end{cases}$$

3. *$\alpha(x)$ is constant: $\alpha(x) = \alpha$.*

As before we take prey birth rate as a separable function $\beta(x, N^*) = \beta(N^*)\beta_0(x)$ with $\beta_0(x) = \chi_{[A,\infty)}$. This assumptions model a predator which feeds selectively only on larger reproductive prey sizes. In what follows we show that in this case oscillations also occur. To see that, we take $g(x) = 1$ and $\mu'(N^*) = 0$. We start again from system (4.27). Solving the differential equation we obtain

$$\xi(x) = \xi(0)\pi(\lambda; x, P^*) - \eta u(0)\pi(\lambda; x, P^*)\gamma(x)\frac{1}{\lambda}[e^{\lambda x} - e^{\lambda A}]. \tag{4.40}$$

Computing the integral of ξ we have

$$\begin{aligned} \int_A^\infty \xi(x)dx &= \xi(0)e^{-(\lambda+\mu)A}\frac{1}{\lambda+\mu+\gamma P^*} - \frac{\eta u(0)\gamma}{\lambda}e^{-\mu A}\left[\frac{1}{\mu+\gamma P^*} - \frac{1}{\lambda + mu + \gamma P^*}\right] \\ &= \xi(0)e^{-(\lambda+\mu)A}\frac{1}{\lambda+\mu+\gamma P^*} - -\frac{\eta d}{\alpha(\lambda+\mu+\gamma P^*)} \end{aligned} \tag{4.41}$$

where we have used the equilibrium equation $\alpha\gamma u(0)e^{-\mu A} = d(\mu + \gamma P^*)$. Substituting in the equation for η in (4.27) we obtain the following formula for η:

$$\eta = \frac{\xi(0)\alpha\gamma P^* e^{-(\lambda+\mu)A}}{\lambda^2 + L\lambda + K} \tag{4.42}$$

where $L = \mu + \gamma P^*$ and $K = \gamma P^* d$. The integrals of ξ are given by:

$$\int_A^\infty \xi(x)dx = \xi(0)\frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2+L\lambda+K} \qquad \int_0^\infty \xi(x)dx = \frac{\xi(0)}{\lambda+\mu}\left(1 - e^{-(\lambda+\mu)A}\right) \tag{4.43}$$

Substituting in the equation for $\xi(0)$, and canceling $\xi(0)$ we obtain the following *characteristic equation*:

$$1 = \beta(N^*)\frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2+L\lambda+K} + F\left[\frac{1}{\lambda+\mu}\left(1 - e^{-(\lambda+\mu)A}\right) + \frac{\lambda e^{-(\lambda+\mu)A}}{\lambda^2+L\lambda+K}\right]. \tag{4.44}$$

The above characteristic equation simplifies to

$$(\lambda + \mu - F)(\lambda^2 + L\lambda + K) = [\beta(N^*)\lambda(\lambda+\mu) - F\gamma P^*(\lambda+d)]e^{-(\lambda+\mu)A}.$$

Using the corresponding equation for the equilibria:

$$e^{-\mu A}\beta(N^*) = \mu + \gamma P^* \tag{4.45}$$

the characteristic equation takes the form:

$$(\lambda + \mu - F)(\lambda^2 + L\lambda + K) = L[\lambda(\lambda+\mu) - V\gamma P^*)(\lambda+d)]e^{-\lambda A} \tag{4.46}$$

where $V = F/\beta(N^*)$. Furthermore, the characteristic equation can be rewritten as:

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = [T_1\lambda^2 + T_2\lambda + T_3]e^{-\lambda A} \tag{4.47}$$

where

$$\begin{aligned} a_1 &= \mu - F + L & T_1 &= L \\ a_2 &= L(\mu - F) + K & T_2 &= L(\mu - V\gamma P^*) \\ a_3 &= (\mu - F)K & T_3 &= LVK \end{aligned} \tag{4.48}$$

Techniques similar to the ones used in the appendix to establish oscillations in Theorem 4.3 can be used in the case of characteristic equation (4.47) to yield with some additional assumptions the following result:

Result: *Assume Assumptions 4.2. Additional assumption corresponding to (4.39) may apply. Then the roots of the characteristic equation (4.47) undergo Hopf bifurcation and the system (2.4) exhibits sustained oscillations with the predator and the prey coexisting.*

A finite difference method can be used to simulate model (2.4). To find parameters that would produce oscillations, we let $\lambda = \xi + wi$ and separate the real and imaginary part in (4.46). We let $\xi = 0.001$. We further assign values to some of the parameters. Thus, we assign $\mu = 0.1$, $-F = 1$, and $A = 1$. We also take $\beta(x, N^*) = \bar{\beta}\chi_{[A,\infty)}e^{-cN^*}$. For a given w the system for the real and the imaginary part becomes a linear system in γP^*, and $d\gamma P^*$. We solve that linear system using Mathematica, and we obtain $\gamma P^* = f_1(w)$ and $d\gamma P^* = f_2(w)$ as functions of w. The parametric plot of these two functions in the (γP^*,$d\gamma P^*$) plane is given in Figure 6. For $w = 3.96055$ we obtain the following *positive* values for $\gamma P^* = 0.35$ and $d\gamma P^* = 16.3689$. That gives a value for $d = 46.7682857$. Using the equations for the equilibria, we determine that $\bar{\beta} = 9.62023$, $c = 1$, and $\alpha = 23.2591$. The parameter γ is determined so that predator's reproduction number is larger than one. In particular, we took, $\gamma = 1$. The resulting oscillations of the predator and the prey are presented in Figure 7.

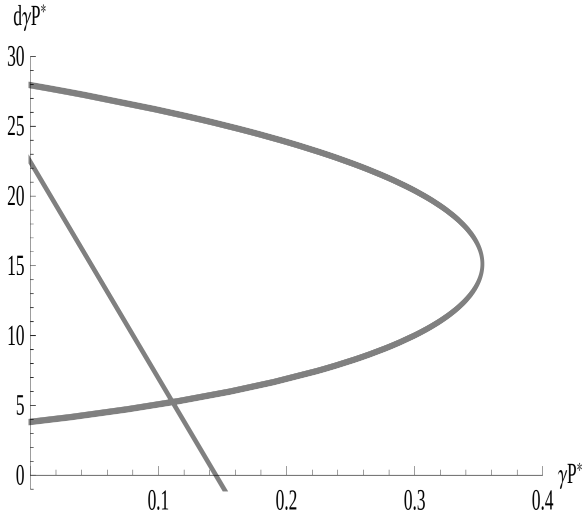

FIGURE 6. Parametric plot in the (γP^*,$d\gamma P^*$).

5. DISCUSSION

In this article we introduce a non-linear predator-prey model where the prey is structured by size. The main question that we address is whether predation on a size-structured prey can be responsible for the sustained oscillations observed in the predator-prey dynamics in nature. We consider two main aspects:

1. We show that the presence of a predator which predates on a size-structured prey can destabilize an otherwise stable equilibrium of the prey, even if the predation of the predator is size non-specific.

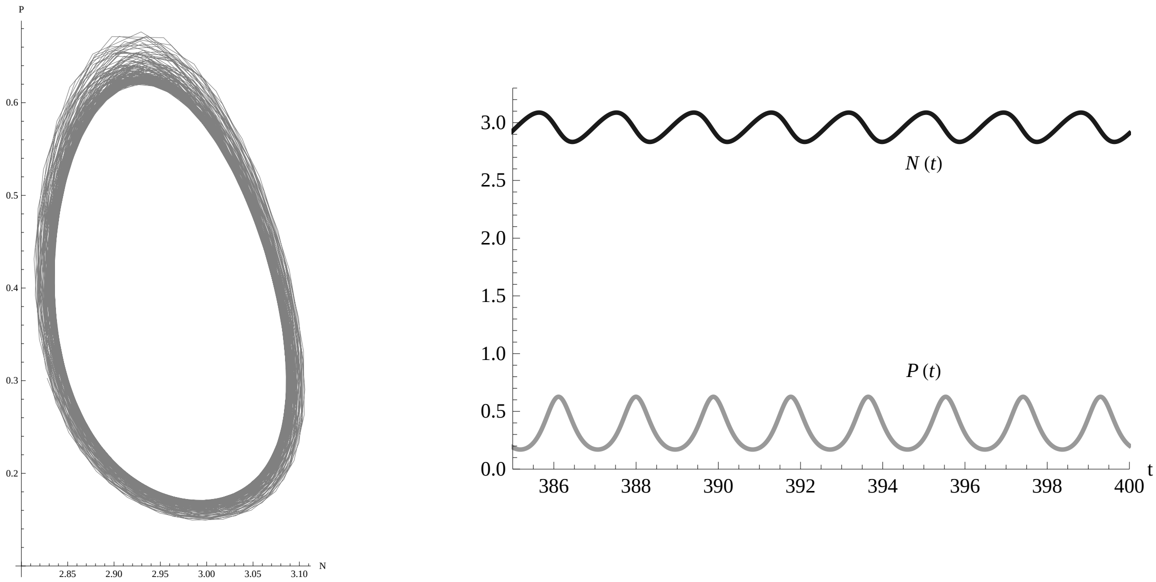

FIGURE 7. The left figure shows the cycle in the $(N,\, P)$ plane with time as a parameter. The right figure shows the oscillations in the total number of prey and the predator as functions of time when those oscillations have stabilized.

(2) We show that size-specific predation is capable of producing oscillations in the predator-prey dynamics. We find that can be the case by examining a scenario when the predator predates on the reproductive sizes of the prey only.

To address the main question we first examine the dynamics of the corresponding ODE model, where the prey is homogeneous with respect to size. We find that the ODE model has an extinction equilibrium, can potentially have multiple prey-only equilibria, and a unique predator-prey coexistence equilibrium. The coexistence equilibrium is locally asymptotically stable if the prey's growth rate decreases with the increase of the prey population. If, however, prey growth rate exhibits Allee effect, then the predator-prey coexistence equilibrium can become destabilized and oscillations are possible. To rule out that this scenario is responsible for the oscillations in the size-structured model, we assume in most cases that the prey birth rate declines with the population size.

The size-structured model also has an extinction equilibrium and multiple prey-only equilibria. We could not rule out the possibility that multiple coexistence equilibria exist. To interpret conditions for existence of equilibria we define net reproduction rate of the prey population as a function of the prey population size $\mathcal{R}(N)$, and intrinsic reproduction number of the prey population $\mathcal{R}_0$, defined as the value of the net reproduction rate when the prey population size is zero. We find that if $\mathcal{R}_0 > 1$ there is always at least one prey-only equilibrium. If $\mathcal{R}_0 < 1$ then there may be no prey-only equilibria, or there may be an even number of prey-only equilibria, if they are all simple. Furthermore, we define predator reproduction at the N_j^* prey-only equilibrium. Conditions on the predator reproduction number guarantee existence of a predator-prey coexistence equilibrium.

We find that the extinction equilibrium is locally stable if $\mathcal{R}_0 < 1$ and unstable otherwise. The extinction equilibrium cannot be globally stable because of the presence of subthreshold equilibria. Furthermore, we find that the jth prey-only equilibrium $\mathcal{E}_j$ is unstable if the reproduction number of the predator at the jth only equilibrium $\mathcal{R}_{p,j} > 1$. Of the prey-only equilibria for which $\mathcal{R}_{p,j} < 1$ holds, the ones for which the net reproduction rate of the prey satisfies $\mathcal{R}'(N_j^*) > 0$ are also unstable. The key result on stability of prey-only equilibria says that if the death rate is size independent and increasing with prey population size, while the birth rate is decreasing with population but may depend on individuals' size in an arbitrary fashion, then the prey-only equilibrium is stable.

We investigated the stability of the coexistence equilibria in two cases. In the first case all rates are constant with respect to individuals' size, except the birth rate which may be arbitrary. For exponential in size birth rate we show that the coexistence equilibrium is locally asymptotically stable. However, if the predator predates uniformly on all sizes, but only mature individuals reproduce, then even if the prey's birth rate is decreasing with the prey's total population size, then the coexistence equilibrium may become unstable, and Hopf bifurcation occurs. We note that in these conditions, if all sizes of the prey reproduced uniformly, then oscillations would not have occurred. In the second case, all rates are constant with exception of the predation rate and prey birth rate. In this case we allow the predator to predate on individuals of reproductive size. We conclude that the predator-prey equilibrium can become unstable and oscillations are possible. Thus, the answer to our main question whether size-specific predation can destabilize the predator-prey dynamics is "yes". The idea of size-specific predation destabilizing the dynamics is somewhat paradoxal as size may permit size refuges for the prey from predation which may seem stabilizing. However, evolution of the prey to more advantageous sizes, not preyed on by the predator, happens on evolutionary scale which may be much slower than the time the predator needs to adapt to preying on different sizes. In a recent article Mougi and Iwasa [9] find that if the predator's trait evolves faster than the prey's, oscillations are possible and likely. In other words, size is only a *temporary* escape mechanism for the prey and as such may be responsible for the oscillatory dynamics [10].

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APPENDIX

Proof of Theorem 4.3. Throughout this proof we will consider the special case when $g(x) = 1$. With this form of the birth rate, we can integrate the integral in the right-hand size of the characteristic equation (4.34). With the assumption that $\mu' = 0$, and the denominator in the form (4.35), the characteristic equation becomes:

$$1 - \frac{F\lambda^2}{(\lambda + \mu + \gamma P^*)(\lambda^2 + R)} = \frac{\beta(N^*)}{\lambda + \mu + \gamma P^*} e^{-(\lambda+\mu+\gamma P^*)A} \tag{5.1}$$

We note that the equation for the equilibria implies that

$$\mu + \gamma P^* = \beta(N^*)e^{-(\mu+\gamma P^*)A}$$

Hence, the characteristic equation simplifies to

$$\lambda + \eta - \frac{F\lambda^2}{\lambda^2 + R} = \eta e^{-\lambda A} \tag{5.2}$$

where $\eta = \mu + \gamma P^*$. Lemma 4.5 implies that for $A = 0$ (with $\rho = 0$) the above equation has only roots with negative real parts and the coexistence equilibrium is locally stable. As a first step to establishing Hopf bifurcation for some $A_0 > 0$, we look for purely imaginary solutions of the simplified characteristic equation (5.2). Set $\lambda = i\omega$. The equation (5.2) becomes

$$i\omega + \eta + \frac{F\omega^2}{R - \omega^2} = \eta e^{-i\omega A}$$

Separating the real and imaginary part in the above equation, we obtain that ω should satisfy the following system:

$$\begin{aligned} \eta + \frac{F\omega^2}{R - \omega^2} &= \eta \cos(\omega A) \\ \omega &= -\eta \sin(\omega A) \end{aligned}$$

We eliminate the trigonometric functions by squaring both sides of the each equation above, and adding the equations. Thus, ω should satisfy the following equation

$$\left(\eta + \frac{F\omega^2}{R - \omega^2}\right)^2 + \omega^2 = \eta^2. \tag{5.3}$$

We set $\omega^2 = z$ to obtain

$$\left(\eta + \frac{Fz}{R - z}\right)^2 + z = \eta^2. \tag{5.4}$$

Rewriting the above equation as a polynomial equation in z we obtain

$$z[z^2 - (2\eta F - F^2 + 2R)z + (R^2 + 2\eta RF)] = 0$$

Assumption (4.39) guarantees that the above equation has three real roots: a negative one, zero, and a positive one. Let $z_0 = \omega_0^2$ be the positive root. Then $\omega_0 = \sqrt{z_0}$. To complete the bifurcation analysis, we choose the maturation size A as a bifurcation parameter. We view the solutions of the characteristic equation (5.2) as functions of the parameter A, namely $\lambda(A) = \rho(A) + i\omega(A)$. For some value A_0 we have $\rho(A_0) = 0$, and $\omega(A_0) = \omega_0$. We need to show that the roots cross the imaginary axis with non-zero speed, that is we need to show that

$$\frac{d\Re\lambda(A)}{dA}|_{A=A_0} > 0.$$

To see this last inequality, we differentiate the characteristic equation (5.2) with respect to the bifurcation parameter A to obtain:

$$\left[1 + \eta A e^{-\lambda A} - \frac{2FR\lambda}{(\lambda^2 + R)^2}\right] \frac{d\lambda}{dA} = -\eta\lambda e^{-\lambda A}.$$

To simplify the computation, we look at the inverse of $\frac{d\lambda(A)}{dA}$:

$$\left(\frac{d\lambda}{dA}\right)^{-1} = \frac{1-\frac{2FR\lambda}{(\lambda^2+R)^2}}{-\eta\lambda e^{-\lambda A}} - \frac{A}{\lambda} \tag{5.5}$$

$$= \frac{1-\frac{2FR\lambda}{(\lambda^2+R)^2}}{-\lambda\left(\lambda+\eta-\frac{F\lambda^2}{\lambda^2+R}\right)} - \frac{A}{\lambda} \tag{5.6}$$

We set $\lambda = i\omega_0$ and rationalize the denominator:

$$\left(\frac{d\lambda}{dA}\right)^{-1}|_{\lambda=i\omega_0} = \frac{1-\frac{2FRi\omega_0}{(-\omega_0^2+R)^2}}{-i\omega_0\left(i\omega_0+\eta+\frac{F\omega_0^2}{-\omega_0^2+R}\right)} - \frac{A}{i\omega_0} \tag{5.7}$$

$$= \frac{\left[1-\frac{2FRi\omega_0}{(-\omega_0^2+R)^2}\right]\left(-i\omega_0+\eta+\frac{F\omega_0^2}{-\omega_0^2+R}\right)}{-i\omega_0\left(\omega_0^2+\left(\eta+\frac{F\omega_0^2}{-\omega_0^2+R}\right)^2\right)} + \frac{Ai}{\omega_0}$$

We take the real part of the expression in the right-hand side and using (5.3) we obtain:

$$\Re\left(\frac{d\lambda}{dA}\right)^{-1} = \frac{1}{\eta^2}\left[\frac{2FR}{(R-\omega_0^2)^2}\left(\eta+\frac{F\omega_0^2}{R-\omega_0^2}\right)+1\right] \tag{5.8}$$

The expression on the right hand side is not automatically positive since $F < 0$. To see its positivity, we recall that $\omega_0^2 = z_0$, and z_0 is the rightmost solution of the equation $h(z) = \eta^2$ where

$$h(z) = \left(\eta+\frac{Fz}{R-z}\right)^2 + z.$$

We observe that, since z_0 is the positive root of the equation,

$$z_0 = R + \frac{2\eta F - F^2 + \sqrt{(2\eta F - F^2)^2 - 4RF^2}}{2} < R.$$

Hence this z_0 is on left of R. In addition $h(z)$ has only one asymptote at $z = R$. Hence the function is continuous between 0 and R. Furthermore, the first derivative of this function is given by

$$h'(z) = \frac{2FR}{(R-z)^2}\left(\eta+\frac{Fz}{R-z}\right)+1 \tag{5.9}$$

Note that

$$h'(0) = \frac{R^2+2\eta RF}{R^2} < 0$$

by assumption and clearly $h(z) \to +\infty$ as $z \to R^-$. Since $h(z)$ cannot have more than one positive root other than z_0, we have that $h'(z_0) > 0$, that is

$$\frac{2FR}{(R-z_0)^2}\left(\eta+\frac{Fz_0}{R-z_0}\right)+1 > 0. \tag{5.10}$$

The last inequality implies that

$$\left(\frac{d\Re\lambda}{dA}\right)^{-1}|_{A=A_0} > 0.$$

This completes the proof.

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Department of Mathematics, University of Florida, 358 Little Hall, PO Box 118105, Gainesville, FL 32611–8105
E-mail address: `souvik@math.ufl.edu`

Department of Mathematics, University of Florida, 358 Little Hall, P.O. Box 118105, Gainesville, FL 32611-8105
E-mail address: `maia@ufl.edu`