COEXISTENCE AND ASYMPTOTIC STABILITY IN STAGE-STRUCTURED PREDATOR-PREY MODELS

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Abstract. In this paper we analyze the effects of a stage-structured predator-prey system where the prey has two stages, juvenile and adult. Three different models (where the juvenile or adult prey populations are vulnerable) are studied to evaluate the impacts of this structure to the stability of the system and coexistence of the species. We assess how various ecological parameters, including predator mortality rate and handling times on prey, prey growth rate and death rate, prey capture rate and nutritional values in two stages, affect the existence and stability of all possible equilibria in each of the models, as well as the ultimate bounds and the dynamics of the populations. The main focus of this paper is to find general conditions to ensure the presence and stability of the coexistence equilibrium where both the predator and prey can co-exist Through specific examples, we demonstrate the stability of the trivial and co-existence equilibrium as well as the dynamics in each system.

1. **Introduction.** Various ecological models have been developed in form of differential equation systems to study predator-prey interactions with effects of diffusion, functional responses, time delays and stage-structure (see, for a few examples, [2, 7, 4, 8, 9, 10, 11, 12, 13, 15, 17, 20, 22]). It has also been realized that the changes of a certain organism has an impact on the food chain with which it is involved. If an organism grows radically throughout its life cycle, the amount it eats, and the amount of it which can be consumed by its predator, if it has one, will most likely change as well. For this reason, researches regarding non-homogeneous populations have started to appear in the last forty years [6, 14, 16, 18, 20]. Various work has been done where stage-structure is used on predator [2, 3, 21] and prey [1, 5, 14, 20].

In 1983, Hastings [14] introduced differential equation models with a stage-structured prey, which are similar to the ones studied in our paper. In 2005, Abrams and Quince [1] used Hastings models to analyze the impact of mortality on predator population size and stability in systems with stage-structured prey, under a simplified condition where the adult prey and juvenile prey have the same relative nutritional value ($e_1 = e_2 = 1$) to the predator. Two of the special cases they

considered are: only juvenile prey are vulnerable and only adult prey are vulnerable, which are both extreme cases for the stage-structured model. Although there are many examples in nature where a predator will mostly consume only young prey, usually due to the dangers of attacking the larger adult prey, there are still times even in these scenarios where the predator will attack the adult prey. Possible explanations for this include vulnerability of the adult prey, desperation of the predator, or teamwork of several predators. For this reason, it is also important to consider the generalized model where both young and adult prey are vulnerable, with various ecological parameters included.

The analysis that is given in this paper focuses on predator-prey systems, in which the prey has two-stages (juvenile and adulthood), and the predator has one. The system is described by the following system of equations:

$$\frac{dN_1}{dt} = b_2 N_2 - d_1 N_1 - g N_1 - s_1 N_1 P H(e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)$$
$$\frac{dN_2}{dt} = g N_1 - d_2 N_2 - s_2 N_2 P H(e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2) \qquad (1)$$
$$\frac{dP}{dt} = P((e_1 s_1 N_1 + e_2 s_2 N_2) * H(e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2) - D)$$

where the variables, functions and parameters are defined as follows: N_1 and N_2 are the population densities of juvenile and adult prey, P is the population density of the predator, b_2 is the per capita birth rate of adult prey (producing new offsprings for juvenile prey) , which is presented as a constant here since the model assumes density-independent prey growth, d_1 and d_2 are parameters giving the per capita death rates of juvenile and adult prey, D is the per capita death rate of the predator, g is the per capita transition rate of juveniles to adults in the prey population, s_i is the per capita capture rate of prey in class i by a searching predator, h_i is the predator's handling time of prey of class i and e_i represents the relative nutritional value of an individual of prey type i to the predator. H is the Holling Type II function describing predator satiation defined as: $H(N) = \frac{1}{1+N}$ [1].

The focus of this paper is to analyze three different models utilizing stage structures on the prey while the juveniles, or adults, or both are vulnerable to the predator. We find the conditions to ensure the existence and asymptotic stability of the equilibrium points, especially the one where both the predator and prey can co-exist. The main goal is to show, in each of these models, how the ecological parameters (the birth rate, death rate and transition rate of the prey; the mortality rate of the predator; the predator capture rates, handling times, and relative nutritional values for different prey stages) affect the dynamics of the populations. For this purpose, we will consider three possible equilibrium points: $(0, 0, 0)$, $(N_1, N_2, 0)$, and (N_1, N_2, P), which represent different ecological outcomes in the system. for the special cases where prey is only vulnerable at one stage, we give explicit stability conditions and further analysis on the effect of various parameters. These results are consistent with the discussions in [1] under specific assumptions for certain parameters. For the general model where prey is vulnerable at both stages, we obtain, for the first time, the coexistence equilibrium of the model through the population ratio of adult prey to juvenile prey. This expression also enables us to further analyze the Jacobian matrix of the system and find conditions for local asymptotic stability and instability of the coexistence equilibrium. Furthermore, we utilize the comparison argument and method of upper-lower solutions to investigate the global stability of the trivial equilibrium (for extinction) and the exponential bounds of

the populations when the coexistence equilibr1um is in presence. Each of our main results is accompanied by an example of numerical simulations, and the ecological interpretations of the mathematical analysis are given in the discussion/conclusion section at the end of the article.

2. **The ultimate bounds for the populations.** In this section we obtain some preliminary results on upper-bound functions for the predator and prey populations. These bounds will provide crucial information on extinction and exponential convergence of the species. In general, the population dynamics in the stage-structured predator-prey model (1) depends on many ecological parameters. However, in this section we see that the relation within a few parameters can determine the ultimate ecological outcome of the system.

2.1. **Extinction of the predator by death rate and prey handling time.** Our first result is about the ultimate bound of the predator population. From the third equation in (1),

$$
\begin{aligned}
\frac{dP}{dt} &= P\left(\frac{e_1 s_1 N_1 + e_2 s_2 N_2}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2} - D\right) \\
&\leq P\left(\frac{e_1 s_1 N_1 + e_2 s_2 N_2}{1 + \underline{h}(e_1 s_1 N_1 + e_2 s_2 N_2)} - D\right) \\
&\leq P\left(\frac{1 - D\underline{h}}{\underline{h}}\right)
\end{aligned}
\tag{2}
$$

where $\underline{h} = \min\{h_1, h_2\}$. This implies that

Theorem 2.1. *If $Dh_1 > 1$ and $Dh_2 > 1$, then the predator population in model (1) will go to extinction exponentially.*

- $0 \leq P(t) \leq P(0)e^{-\left(\frac{D\underline{h}-1}{\underline{h}}\right)t}$, *with $\underline{h} = \min\{h_1, h_2\}$.*

2.2. **Extinction of the total population by birth and death rate of the adult prey.** Let $F(t) = N_1(t) + N_2(t) + P(t)$ be the total population of the three species in model (1). Based on the fact that the relative nutritional values for the preys $0 < e_1, e_2 \leq 1$, the summation of the three equations in (1) gives:

$$
\begin{aligned}
\frac{dF}{dt} &= (b_2 - d_2)N_2 - d_1 N_1 - P\left(\frac{(1-e_1)s_1 N_1 + (1-e_2)s_2 N_2}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2} + D\right) \\
&\leq (b_2 - d_2)N_2 - d_1 N_1 - DP \\
&\leq -\delta F
\end{aligned}
\tag{3}
$$

where $\delta = \min\{d_2 - b_2, d_1, D\}$. This implies that

$$
0 \leq F(t) \leq F(0)e^{-\delta t}.
$$

Theorem 2.2. *If $d_2 > b_2$, then all three populations in model (1) will go to extinction exponentially.*

- $0 \leq N_1(t) + N_2(t) + P(t) \leq [N_1(0) + N_2(0) + P(0)]e^{-\delta t}$, *with $\delta = \min\{d_2 - b_2, d_1, D\} > 0$.*

In this case, the trivial equilibrium $(0,0,0)$ is globally asymptotically stable.

3. **Equilibrium points with extinction of predator.** In this section, we give stability results on the two equilibrium points with absence of the predator population.

3.1. **Equilibrium for extinction of predator and prey.** The Jacobian matrix of the system (1) for the equilibrium $(0, 0, 0)$, with extinction of both predator and prey, is:

$$J(0, 0, 0) = \begin{pmatrix} -d_1 - g & b_2 & 0 \\ g & -d_2 & 0 \\ 0 & 0 & -D \end{pmatrix}$$

The eigenvalues for this matrix are:

- $\lambda_1 = \frac{1}{2}(-\sqrt{(d_1 + d_2 + g)^2 - 4(d_1 d_2 + d_2 g - b_2 g)} - d_1 - d_2 - g)$,
- $\lambda_2 = \frac{1}{2}(\sqrt{(d_1 + d_2 + g)^2 - 4(d_1 d_2 + d_2 g - b_2 g)} - d_1 - d_2 - g)$,
- $\lambda_3 = -D$.

If $b_2 g > d_2(d_1 + g)$ then λ_2 is a positive real number, which indicates that the trivial equilibrium is an unstable saddle point.

In order to investigate the global asymptotic stability, we define a pair of upper-lower solutions [19] $(\tilde{N}_1, \tilde{N}_2, \tilde{P})$ and $(\hat{N}_1, \hat{N}_2, \hat{P})$ for system (1) satisfying the following differential inequalities:

$$
\begin{aligned}
\frac{d\tilde{N}_1}{dt} &\geq b_2 \tilde{N}_2 - d_1 \tilde{N}_1 - g\tilde{N}_1 - s_1 \tilde{N}_1 \hat{P} H(e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2) \\
\frac{d\tilde{N}_2}{dt} &\geq g\tilde{N}_1 - d_2 \tilde{N}_2 - s_2 \tilde{N}_2 \hat{P} H(e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2) \\
\frac{d\tilde{P}}{dt} &\geq \tilde{P}[(e_1 s_1 \tilde{N}_1 + e_2 s_2 \tilde{N}_2) * H(e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2) - D] \\
\frac{d\hat{N}_1}{dt} &\leq b_2 \hat{N}_2 - d_1 \hat{N}_1 - g\hat{N}_1 - s_1 \hat{N}_1 \tilde{P} H(e_1 s_1 h_1 \hat{N}_1 + e_2 s_2 h_2 \hat{N}_2) \\
\frac{d\hat{N}_2}{dt} &\leq g\hat{N}_1 - d_2 \hat{N}_2 - s_2 \hat{N}_2 \tilde{P} H(e_1 s_1 h_1 \hat{N}_1 + e_2 s_2 h_2 \hat{N}_2) \\
\frac{d\hat{P}}{dt} &\leq \hat{P}[(e_1 s_1 \hat{N}_1 + e_2 s_2 \hat{N}_2) * H(e_1 s_1 h_1 \hat{N}_1 + e_2 s_2 h_2 \hat{N}_2) - D].
\end{aligned}
\tag{4}
$$

and with $(\tilde{N}_1(t), \tilde{N}_2(t), \tilde{P}(t)) \geq (\hat{N}_1(t), \hat{N}_2(t), \hat{P}(t))$ for all $t \geq 0$. It is well-known by comparison arguments in differential equation systems [19] that if there exists a pair of upper-lower solutions, then the solution of (1) satisfies $(\tilde{N}_1(t), \tilde{N}_2(t), \tilde{P}(t)) \geq (N_1(t), N_2(t), P(t)) \geq (\hat{N}_1(t), \hat{N}_2(t), \hat{P}(t))$ for all $t > 0$ as long as $(\tilde{N}_1(0), \tilde{N}_2(0), \tilde{P}(0)) \geq (N_1(0), N_2(0), P(0)) \geq (\hat{N}_1(0), \hat{N}_2(0), \hat{P}(0))$.

The three inequalities in (4) for lower solution can be satisfied by setting

$$(\hat{N}_1(t), \hat{N}_2(t), \hat{P}(t)) = (0, 0, 0).$$

It then suffices to look for upper solutions $(\tilde{N}_1(t), \tilde{N}_2(t), \tilde{P}(t))$ with

$$
\begin{aligned}
\frac{d\tilde{N}_1}{dt} &= b_2 \tilde{N}_2 - d_1 \tilde{N}_1 - g\tilde{N}_1 \\
\frac{d\tilde{N}_2}{dt} &= g\tilde{N}_1 - d_2 \tilde{N}_2 \\
\frac{d\tilde{P}}{dt} &= \tilde{P}[(e_1 s_1 \tilde{N}_1 + e_2 s_2 \tilde{N}_2) * H(e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2) - D]
\end{aligned}
$$

From here we obtain that

$$(\tilde{N}_1(t), \tilde{N}_2(t))^T = e^{At}(N_1(0), N_2(0))^T,$$

where

$$A = \begin{pmatrix} -d_1 - g & b_2 \\ g & -d_2 \end{pmatrix}$$

The eigenvalues for A are listed as λ_1 and λ_2 for $J(0,0,0)$. If $b_2 g < d_2(d_1 + g)$, then both eigenvalues are either negative real numbers or complex numbers with negative real parts. In this case, we have $(\tilde{N}_1(t), \tilde{N}_2(t))^T \to (0,0)^T$ as $t \to \infty$. For any positive ϵ, there exists a $T_\epsilon > 0$ such that

$$\frac{d\tilde{P}}{dt} = \tilde{P}[(e_1 s_1 \tilde{N}_1 + e_2 s_2 \tilde{N}_2) * H(e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2) - D] < -\epsilon \tilde{P}$$

for $t > T_\epsilon$. This also implied that $\tilde{P}(t) \to 0$ as $t \to \infty$. Hence we have

Theorem 3.1. *The trivial equilibrium* $(0,0,0)$ *in system (1) is*

- *unstable if* $b_2 g > d_2(d_1 + g)$,

- *globally asymptotically stable if* $b_2 g < d_2(d_1 + g)$.

We now illustrate the asymptotic stability of the trivial equilibria $(0,0,0)$ through numerical simulations of model (1), with parameters: $\{b_2 = 0.6, g = 0.2, d_1 = 0.3, d_2 = 0.4, e_1 = 0.5, e_2 = 1.0, s_1 = 0.6, s_2 = 0.3, h_1 = 0.1, h_2 = 0.2, D = 0.1\}$. These ecological parameters satisfy $b_2 g < d_2(d_1 + g)$, so the trivial equilibria $(0,0,0)$ is globally asymptotically stable. With initial populations $N_1(0) = 2.5, N_2(0) = 2.0$, $P(0) = 0.7$, the numerical simulation of model (1) demonstrated in Figure 1 shows the extinction of all species.
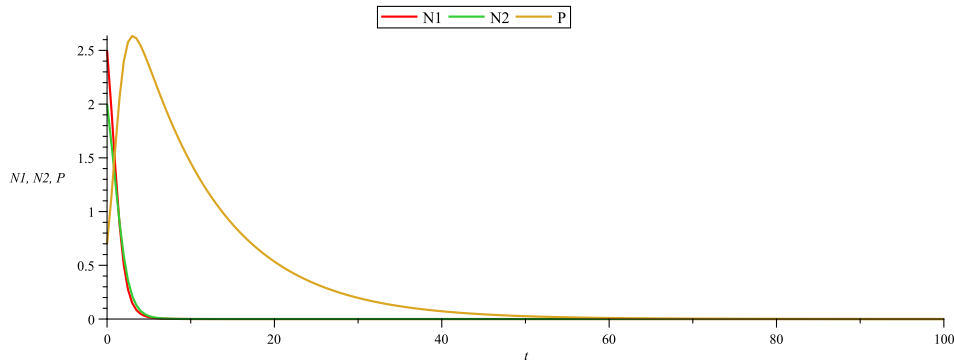

FIGURE 1. Stability of Trivial Equilibrium

3.2. **Equilibrium for extinction of predator only.** We will next consider the equilibrium points with extinction of the predator $(N_1, N_2, 0)$. The positive population sizes N_1 and N_2 must satisfy:

- $b_2 N_2 - d_1 N_1 - g N_1 = 0$ and $g N_1 - d_2 N_2 = 0$.

This is a system of dependent equations so there will be an infinite number of solutions $N_1 = \frac{d_2 N_2}{g}$ if $b_2 g = d_2(d_1 + g)$ and no solution if $b_2 g \neq d_2(d_1 + g)$.

Under the assumption of $b_2 g = d_2(d_1 + g)$, there are infinite number of equilibria and asymptotic stability cannot occur. The Jacobian Matrix for $(\frac{d_2 N_2}{g}, N_2, 0)$ is:

$$\begin{pmatrix} -d_1 - g & b_2 & -\dfrac{N_2 b_2 s_1}{d_1 + g + e_1 s_1 h_1 b_2 N_2 + e_2 s_2 h_2 N_2 d_1 + e_2 s_2 h_2 N_2 g} \\ g & -d_2 & -\dfrac{s_2 N_2 (d_1 + g)}{d_1 + g + e_1 s_1 h_1 b_2 N_2 + e_2 s_2 h_2 N_2 d_1 + e_2 s_2 h_2 N_2 g} \\ 0 & 0 & -\dfrac{e_1 s_1 b_2 N_2 (h_1 D - 1) + e_2 s_2 N_2 (d_1 + g)(h_2 D - 1) + D(d_1 + g)}{d_1 + g + e_1 s_1 h_1 b_2 N_2 + e_2 s_2 h_2 N_2 d_1 + e_2 s_2 h_2 N_2 g} \end{pmatrix}$$

The eigenvalues of this matrix are:

- $\lambda_1 = -(d_1 + d_2 + g) < 0$,
- $\lambda_2 = 0$,
- $\lambda_3 = \dfrac{e_1 s_1 b_2 N_2 (1 - Dh_1) + e_2 s_2 N_2 (d_1 + g)(1 - Dh_2) - D(d_1 + g)}{d_1 + g + e_1 s_1 h_1 b_2 N_2 + e_2 s_2 h_2 N_2 d_1 + e_2 s_2 h_2 N_2 g}$

Theorem 3.2. *When $b_2 g = d_2(d_1 + g)$, the system (1) has infinite many prey-only equilibria $(\frac{d_2 N_2}{g}, N_2, 0)$. Each equilibrium in this set is unstable if $e_1 s_1 b_2 N_2 (1 - Dh_1) + e_2 s_2 N_2 (d_1 + g)(1 - Dh_2) > D(d_1 + g)$.*

4. **Coexistence while only one stage of the prey is vulnerable.** We now consider the conditions for both the prey and predator to coexist in model (1). First, we will examine a couple of special cases where the prey is vulnerable to the predator at only one stage. After that, we then proceed to the general case.

4.1. **Only juveniles are vulnerable.** Often, in biological systems, the predator is similar in size to the prey, and so attacking adult prey can actually be harmful to the predator. Therefore, in these systems, the predator will only attack juvenile prey. The first case considered here assumes that only the juvenile prey are vulnerable to the predator and is described by the following equations: [1]

$$\begin{aligned} \frac{dN_1}{dt} &= b_2 N_2 - d_1 N_1 - g N_1 - s N_1 P * H(eshN_1) \\ \frac{dN_2}{dt} &= g N_1 - d_2 N_2 \\ \frac{dP}{dt} &= P(es N_1 * H(eshN_1) - D) \end{aligned} \tag{5}$$

Here the H function only takes $eshN_1$ as its parameter and we can drop the subscript 1 from e_1, s_1, and h_1. The population densities in the coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ of (5) are:

$$\begin{aligned} \overline{N}_1 &= \frac{D}{es(1 - Dh)} \\ \overline{N}_2 &= \frac{Dg}{d_2 es(1 - Dh)} \\ \overline{P} &= \frac{g(b_2 - d_2) - d_1 d_2}{d_2 s(1 - Dh)} \end{aligned} \tag{6}$$

The conditions for the existence of a positive equilibrium are:

$$0 < Dh < 1 \text{ and } b_2 g > d_2(d_1 + g) > 0. \tag{7}$$

The Jacobian matrix for this equilibrium in model (5) is:

$$J(\overline{N}_1, \overline{N}_2, \overline{P}) = \begin{pmatrix} \dfrac{-b_2g + hDb_2g - hDd_1d_2 - hDd_2g}{d_2} & b_2 & -\dfrac{D}{e} \\ g & -d_2 & 0 \\ \dfrac{e(1 - Dh)(b_2g - d_1d_2 - d_2g)}{d_2} & 0 & 0 \end{pmatrix}$$

The determinant of $(J(\overline{N}_1, \overline{N}_2, \overline{P}) - \lambda I)$ is: $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3$ where:

- $A_1 = \dfrac{b_2g(1 - Dh)}{d_2} + d_1Dh + gDh + d_2$
- $A_2 = \dfrac{D(b_2g - d_1d_2 - d_2g)(1 - Dh)}{d_2} - Dh(b_2g - d_1d_2 - d_2g)$
- $A_3 = D(b_2g - d_1d_2 - d_2g)(1 - Dh)$

Applying the Routh-Hurwitz criteria for stability, the coexistence equilibrium is asymptotically stable if : $A_1 > 0$, $A_3 > 0$, and $A_1A_2 > A_3$. We first observe that the positivity condition (7) for the equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given in (6) ensures that $A_1 > 0$ and $A_3 > 0$.

$A_1A_2 - A_3 =$

$$\dfrac{D(gb_2 - gd_2 - d_1d_2)}{d_2^2} \left[(1 - Dh - d_2h)(gb_2 - gb_2Dh + gd_2Dh + d_1d_2Dh) - d_2^3h\right]$$

This leads to the following theorem about the stability of the coexistence equilibrium in model (5).

Theorem 4.1. *For the model (5) where only the juvenile prey is vulnerable, there is a unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given by (6) if the conditions in (7) hold. This equilibrium is (locally) asymptotically stable if:*

$$(1 - Dh - d_2h)(gb_2 - gb_2Dh + gd_2Dh + d_1d_2Dh) > d_2^3h, \tag{8}$$

and unstable if

$$(1 - Dh - d_2h)(gb_2 - gb_2Dh + gd_2Dh + d_1d_2Dh) < d_2^3h.$$

In order to show the stability of the coexistence equilibrium while d_2 (the death rate of the adult prey) is sufficiently small, we also observe that

$$A_1A_2 - A_3 > (d_1Dh + gDh + d_2)A_2 - A_3$$

$$= Dh(b_2g - d_1d_2 - d_2g)\left[\dfrac{D(d_1 + g)(1 - Dh)}{d_2} - (d_1Dh + gDh + d_2)\right].$$

Hence we can conclude that $A_1A_2 > A_3$ if $D(d_1 + g)(1 - Dh) > d_2(d_1Dh + gDh + d_2)$, which is equivalent to the condition given in the following corollary:

Corollary 4.1. *If the conditions in (7) hold, then the unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given by (6) in model (5) is (locally) asymptotically stable whenever:*

$$d_2 < \sqrt{D(d_1 + g)(1 - Dh) + \left[\dfrac{Dh(d_1 + g)}{2}\right]^2} - \dfrac{Dh(d_1 + g)}{2}. \tag{9}$$

We now give an example of coexistence in model (5) with numerical simulations. With the following set of ecological parameters: $\{b_2 = 0.8, g = 0.2, d_1 = 0.3, d_2 = 0.2, e = 0.5, s = 0.8, h = 0.1, D = 0.1\}$, the condition (8) for asymptotic stability of

the coexistence equilibrium is ensured by Theorem 4.1. The coexistence equilibrium given by (6) is

$$(\overline{N}_1, \overline{N}_2, \overline{P}) = (0.3367, 0.3367, 0.5050).$$

With initial populations $N_1(0) = 0.2$, $N_2(0) = 0.3$, $P(0) = 0.1$, the numerical simulation of model (4) demonstrated in Figure 2 shows that all three populations converge to the equilibrium values for coexistence.
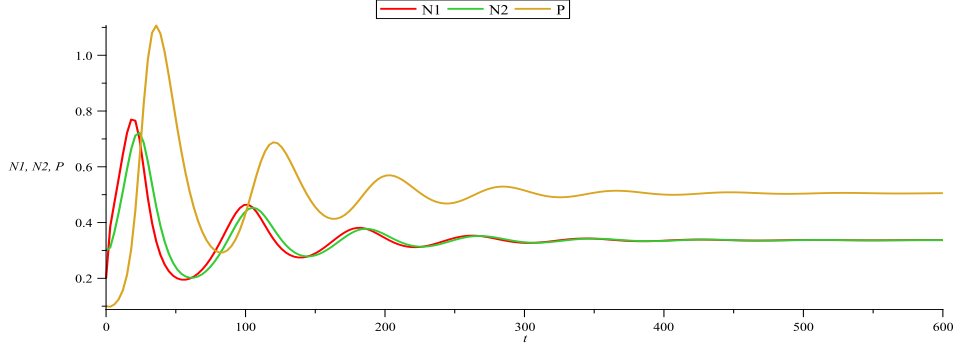

FIGURE 2. Asymptotic Stability, Coexistence While Only Juvenile Vulnerable

4.2. **Only adults are vulnerable.** Another common occurrence in biological systems is when the predator is much larger than its prey. Therefore, it is not efficient for it to consume young prey. Assuming that the predator will only consume adult prey, the second special case considered here is described by the following equations:

$$\frac{dN_1}{dt} = b_2 N_2 - d_1 N_1 - g N_1$$
$$\frac{dN_2}{dt} = g N_1 - d_2 N_2 - s N_2 P * H(eshN_2) \qquad (10)$$
$$\frac{dP}{dt} = P(es N_2 * H(eshN_2) - D)$$

Since this model is assuming that only adult prey is vulnerable to the predator, the H function only takes $eshN_2$ as its parameter. In addition, we can drop the subscript 2 from e_2, s_2, and h_2. The population densities in the coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ of model (10) are:

$$\overline{N}_1 = \frac{b_2 D}{es(1 - Dh)(g + d_1)}$$
$$\overline{N}_2 = \frac{D}{es(1 - Dh)} \qquad (11)$$
$$\overline{P} = \frac{g(b_2 - d_2) - (d_1 d_2)}{s(1 - Dh)(g + d_1)}$$

It is obvious that the conditions in (7) also ensures the positivity of the equilibrium (11) for model (10).

The Jacobian matrix for this equilibrium in model (10) is:

$$J(\overline{N}_1, \overline{N}_2, \overline{P}) = \begin{pmatrix} -d_1 - g & b_2 & 0 \\ g & \dfrac{-b_2 g + hDb_2 g - hDd_1 d_2 - d_2 ghD}{d_1 + g} & -\dfrac{D}{e} \\ 0 & \dfrac{e(1 - Dh)(b_2 g - d_1 d_2 - d_2 g)}{d_1 + g} & 0 \end{pmatrix}$$

Again, the determinant of $(J(\overline{N}_1, \overline{N}_2, \overline{P}) - \lambda I)$ is: $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3$ where:

- $A_1 = \dfrac{b_2 g(1 - Dh)}{d_1 + g} + d_1 + g + d_2 Dh$

- $A_2 = \dfrac{D(b_2 g - d_1 d_2 - d_2 g)(1 - Dh)}{d_1 + g} - Dh(b_2 g - d_1 d_2 - d_2 g)$

- $A_3 = D(b_2 g - d_1 d_2 - d_2 g)(1 - Dh)$

Once again, by applying the Routh-Hurwitz criteria for stability, we see that the coexistence equilibrium is asymptotically stable if : $A_1 > 0$, $A_3 > 0$, and $A_1 A_2 > A_3$. The positivity condition (7) for the equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given in (11) already ensures that $A_1 > 0$ and $A_3 > 0$.

$$A_1 A_2 - A_3 = \frac{D(gb_2 - gd_2 - d_1 d_2)}{(d_1 + g)^2}$$
$$\times \left[(1 - Dh - d_1 h - gh)(gb_2 - gb_2 Dh + gd_2 Dh + d_1 d_2 Dh) - (d_1 + g)^3 h \right]$$

This leads to the following theorem about the stability of the coexistence equilibrium in model (10).

Theorem 4.2. *For the model (10) where only the adult prey is vulnerable, there is a unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given by (11) if the conditions in (7) hold. This equilibrium is (locally) asymptotically stable if:*

$$(1 - Dh - d_1 h - gh)(gb_2 - gb_2 Dh + gd_2 Dh + d_1 d_2 Dh) > (d_1 + g)^3 h. \qquad (12)$$

and unstable if

$$(1 - Dh - d_1 h - gh)(gb_2 - gb_2 Dh + gd_2 Dh + d_1 d_2 Dh) < (d_1 + g)^3 h.$$

For a simplified sufficient condition of stability for coexistence equilibrium, We can also obtain that

$$A_1 A_2 - A_3 > (d_1 + g + d_2 Dh)A_2 - A_3$$
$$= Dh(b_2 g - d_1 d_2 - d_2 g)\left[\frac{Dd_2(1 - Dh)}{d_1 + g} - (d_1 + g + d_2 Dh) \right].$$

From here we conclude that $A_1 A_2 > A_3$ if $Dd_2(1 - Dh) > (d_1 + g)(d_1 + g + d_2 Dh)$, which can hold if the sum of d_1 and g (the death rate of the juvenile and the transition rate of juvenile prey to adult) is sufficiently small. This condition is stated in the following corollary:

Corollary 4.2. *If the conditions in (7) hold, then the unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given by (11) is (locally) asymptotically stable in model (10) whenever:*

$$d_1 + g < \sqrt{Dd_2(1 - Dh) + \left[\frac{d_2 Dh}{2} \right]^2} - \frac{d_2 Dh}{2}. \qquad (13)$$

We also give an example of coexistence in model (10) with numerical simulations. Given the following set of ecological parameters: $\{b_2 = 0.8, g = 0.2, d_1 = 0.3, d_2 = 0.2, e = 1.0, s = 0.3, h = 0.5, D = 0.1\}$, the condition (12) for asymptotic stability of the coexistence equilibrium is ensured by Theorem 4.2. The coexistence equilibrium given by (11) is

$$(\overline{N}_1, \overline{N}_2, \overline{P}) = (0.5442, 0.3401, 0.4082).$$

With initial populations $N_1(0) = 0.2$, $N_2(0) = 0.3$, $P(0) = 0.1$, the numerical simulation of model (10) demonstrated in Figure 3 shows that all three populations converge to the equilibrium values for coexistence.
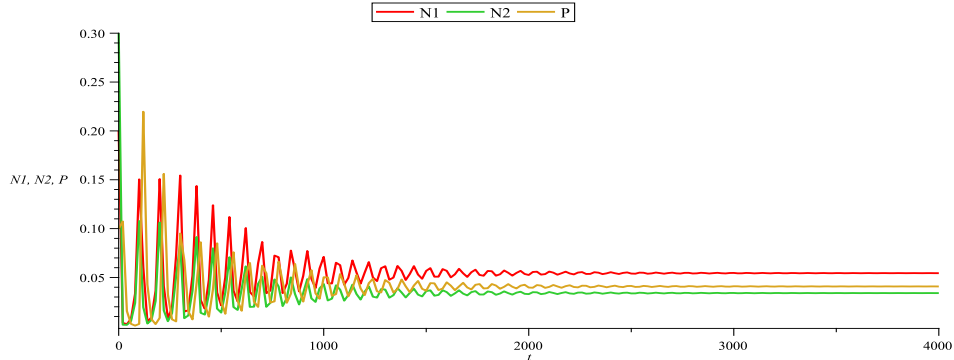
FIGURE 3. Asymptotic Stability, Coexistence While Only Adults Vulnerable

5. **Coexistence while juvenile and adult prey are both vulnerable.** The past two models represent extreme cases in model (1). In general, it is more likely that a predator will consume both the juvenile prey and the adult prey. In addition, the stage-structure in model (1) does play an important role in most predator-prey relationships. Different population densities, physical sizes, and predator handling times for juvenile and adult prey directly affect the dynamics in model (1). Assuming that both juvenile and adult prey are vulnerable to the predator, we explore the nature of the coexistence state and its stability in model (1), with distinct capture rates, handling times and nutritional values which correspond to juvenile and adult prey.

In order to find a component-wise positive equilibrium in model (1), we first assume the restrictions for positivity observed in the two simpler models (5) and (10) still hold:

$$
\begin{aligned}
& b_2 g > d_2(d_1 + g), \\
& 1 - D h_1 > 0, \\
& 1 - D h_2 > 0.
\end{aligned}
\tag{14}
$$

The coexistence equilibrium in model (1) can be solved from the following system of algebraic equations:

$$
\begin{aligned}
& \frac{b_2 N_2 - d_1 N_1 - g N_1}{s_1 N_1} - \frac{g N_1 - d_2 N_2}{s_2 N_2} = 0 \\
& \frac{e_1 s_1 N_1 + e_2 s_2 N_2}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2} - D = 0 \\
& P = \frac{(g N_1 - d_2 N_2)(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)}{s_2 N_2}
\end{aligned}
\tag{15}
$$

From the first equation in system (15), we can obtain the adult-to-juvenile ratio $r = N_2/N_1$ in the prey population :

$$
r = \frac{d_1 s_2 + g s_2 - d_2 s_1 + \sqrt{(d_1 s_2 + g s_2 - d_2 s_1)^2 + 4 g s_1 s_2 b_2}}{2 b_2 s_2} > 0.
\tag{16}
$$

Hence, the population densities in the coexistence equilibrium (N_1, N_2, P) of (1) are:

$$\overline{N}_1 = \frac{D}{e_1 s_1(1 - Dh_1) + re_2 s_2(1 - Dh_2)}$$

$$\overline{N}_2 = r\overline{N}_1 \tag{17}$$

$$\overline{P} = \frac{(g - rd_2)(1 + e_1 s_1 h_1 \overline{N}_1 + re_2 s_2 h_2 \overline{N}_1)}{rs_2}$$

It is obvious that r, $\overline{N}_1$, $\overline{N}_2 > 0$, and $\overline{P} > 0$ if $g - rd_2 > 0$ which means

$$2gb_2 s_2 > d_2 \left(d_1 s_2 + gs_2 - d_2 s_1 + \sqrt{(d_1 s_2 + gs_2 - d_2 s_1)^2 + 4gs_1 s_2 b_2} \right). \tag{18}$$

Noting that condition (18) is equivalent to

$$[2gb_2 s_2 - d_2 (d_1 s_2 + gs_2 - d_2 s_1)]^2 - d_2^2 \left[(d_1 s_2 + gs_2 - d_2 s_1)^2 + 4gs_1 s_2 b_2 \right]$$
$$= 4gb_2 s_2^2(gb_2 - gd_2 - d_1 d_2) > 0, \tag{19}$$

which is ensured by assumption (14). We can now find the following theorem about the coexistence equilibrium in model (1):

Theorem 5.1. *If the conditions $Dh_1 < 1$, $Dh_2 < 1$, and $b_2 g > d_2(d_1 + g)$ hold, then the stage-structured predator-prey model (1) has a unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ given in (17), where r is the adult-to-juvenile ratio in the prey population given in (16).*

The Jacobian Matrix of system (1) for equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P})$ is:

$$J(\overline{N}_1, \overline{N}_2, \overline{P}) = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix}$$

where

$$j_{11} = -d_1 - g - \frac{s_1 P(1 + e_2 s_2 h_2 N_2)}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2},$$

$$j_{12} = b_2 + \frac{e_2 s_1 s_2 h_2 N_1 P}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2},$$

$$j_{13} = -\frac{s_1 N_1}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2},$$

$$j_{21} = g + \frac{e_1 s_1 s_2 h_1 N_2 P}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2},$$

$$j_{22} = -d_2 - \frac{s_2 P(1 + e_1 s_1 h_1 N_1)}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2}, \tag{20}$$

$$j_{23} = -\frac{s_2 N_2}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2},$$

$$j_{31} = \frac{e_1 s_1 P[1 + e_2 s_2(h_2 - h_1)N_2]}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2},$$

$$j_{32} = \frac{e_2 s_2 P[1 + e_1 s_1(h_1 - h_2)N_2]}{(1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2)^2},$$

$$j_{33} = \frac{e_1 s_1 N_1 + e_2 s_2 N_2}{1 + e_1 s_1 h_1 N_1 + e_2 s_2 h_2 N_2} - D.$$

After substituting the coexistence equilibrium (17) into the Jacobian matrix,the determinant of $(J(\overline{N}_1, \overline{N}_2, \overline{P}) - \lambda I)$ is: $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3$ where

$$A_1 = \frac{1}{rs_2(e_1s_1 + re_2s_2)}\{e_2s_2^2r[r(d_2Dh_2 + d_1 + g) + g(1 - Dh_2)]$$
$$+ s_1[e_1s_1(1 - Dh_1) + e_2s_2r](g - rd_2) + e_1s_1s_2(gr + d_1r + g)\};$$

$$A_2 = \frac{\overline{A}_2 - \underline{A}_2}{s_2r^2(e_1s_1 + re_2s_2)} \quad \text{where}$$

$$\overline{A}_2 = s_1(g - rd_2)[e_1s_1(g + rD)(1 - Dh_1) + gre_2s_2(1 - Dh_2)] \tag{21}$$
$$+ e_2s_2^2r^2(g + d_1 + D)[rd_2Dh_2 + g(1 - Dh_2)] + e_1s_1s_2rg(d_1 + g),$$

$$\underline{A}_2 = s_2r^2[b_2g(e_1s_1 + re_2s_2) + re_2s_2] + s_1s_2rD(g - rd_2)[rb_2e_1h_1 + e_2h_2(g - rd_2)];$$

$$A_3 = \frac{1}{s_2r^2(e_1s_1 + re_2s_2)}\{D(g - rd_2)[e_2s_2^2r^2(g + d_1)(1 - Dh_2)$$
$$+ e_1s_1(s_1g + s_2b_2r^2)(1 - Dh_1) + e_2s_1s_2r(1 - Dh_2)(2g - rd_2)]\}.$$

Here r is the adult-to-juvenile ratio in the coexistence equilibrium given by (16). With assumptions in (14), we already know that Dh_1, $Dh_2 < 1$ and $g - rd_2 > 0$, which imply that A_1, $A_3 > 0$. By the Routh-Hurwitz criteria for stability, the coexistence equilibrium in (17) is asymptotically stable if and only if $A_1A_2 > A_3$.

Theorem 5.2. *If the assumptions in (14) hold, then the coexistence equilibrium for model (1) given in (16)-(17) is*

- *(locally) asymptotic stable when $A_1A_2 > A_3$,*
- *unstable when $A_1A_2 < A_3$,*

where A_1, A_2, and A_3 are given in (21).

We now illustrate the dynamics of the populations in model (1) with respect to the presence and stability of the coexistence equilibrium stated in Theorem 5.1 and Theorem 5.2. Consider the following set of parameters: $\{b_2 = 0.8, g = 0.2, d_1 = 0.1, d_2 = 0.2, e_1 = 0.4, e_2 = 0.8, s_1 = 0.8, s_2 = 0.4, h_1 = 0.1, h_2 = 0.2, D = 0.2\}$, which satisfies assumption (14). From Theorem 5.1, the adult-to-juvenile ratio given in (16) is $r = 0.6474$ and the coexistence equilibrium given by (17) is

$$(\overline{N}_1, \overline{N}_2, \overline{P}) = (0.3903, 0.2526, 0.2802).$$

These ecological parameters make $A_1 = 0.8225 > 0$, $A_3 = 0.0241 > 0$, and $A_1A_2 - A_3 = 0.0012 > 0$. Theorem 5.2 indicates that the coexistence equilibrium is (locally) asymptotically stable. The corresponding Jacobian Matrix is:

$$J(\overline{N}_1, \overline{N}_2, \overline{P}) = \begin{pmatrix} -0.5152 & 0.8053 & -0.3035 \\ 0.2009 & -0.3072 & -0.0982 \\ 0.0854 & 0.0837 & 0 \end{pmatrix}$$

The resulting eigenvalues are:

$$-0.8208, \ -0.0008 + 0.1712 * i, \ -0.0008 - 0.1712 * i.$$

Since each of these eigenvalues have negative real part, then the coexistence equilibrium is (locally) asymptotically stable. Figure 4 demonstrates the numerical simulation of model (1) with initial populations $N_1(0) = 0.2$, $N_2(0) = 0.3$, $P(0) = 0.1$.

To demonstrate the dynamic behavior of all the species in model (1) with unstable coexistence equilibrium, we consider another set of parameters: $\{b_2 = 0.8, g = 0.2, d_1 = 0.3, d_2 = 0.2, e_1 = 0.5, e_2 = 1.0, s_1 = 0.6, s_2 = 0.3, h_1 = 0.5, h_2 = 0.8, D = $
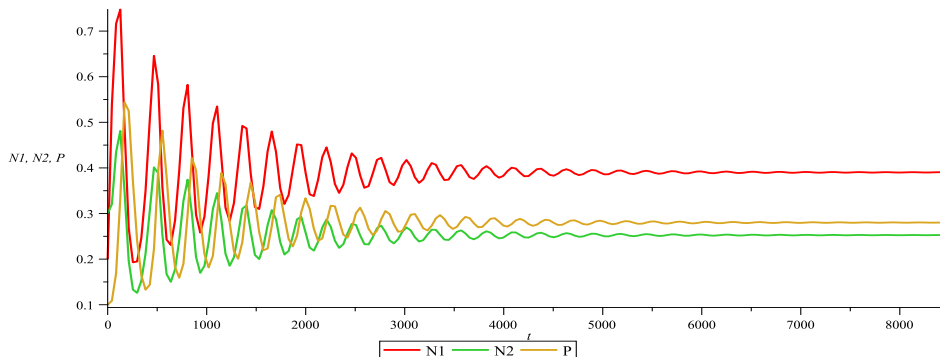
FIGURE 4. Asymptotic Stability, Coexistence While Both Juvenile and Adults Vulnerable

0.2}. These ecological parameters satisfy assumption (14), hence by Theorem 5.1 model (1) has a unique coexistence equilibrium $(\overline{N}_1, \overline{N}_2, \overline{P}) = (0.4304, 0.3325, 0.2248)$. With $A_1 = 0.8661 > 0$, $A_3 = 0.0117 > 0$, and $A1A2 - A3 = -0.0049 < 0$, Theorem 5.2 indicates that the coexistence equilibrium is unstable. The corresponding Jacobian Matrix is:

$$J(\overline{N}_1, \overline{N}_2, \overline{P}) = \begin{pmatrix} -0.6112 & 0.8106 & -0.2257 \\ 0.2026 & -0.2548 & -0.0872 \\ 0.0531 & 0.0495 & 0 \end{pmatrix}$$

The resulting eigenvalues are:

$$-0.8725, \; 0.0032 + 0.1158 * i, \; 0.0032 - 0.1158 * i.$$

Since $\lambda_1 < 0$, λ_2 and λ_3 have positive real parts, then the coexistence equilibrium is an unstable spiral point. Figure 5 demonstrates the numerical simulation of model (1) with initial populations $N_1(0) = 0.2$, $N_2(0) = 0.3$, $P(0) = 0.1$. All three of the species have their population sizes oscillating with increasing magnitude.
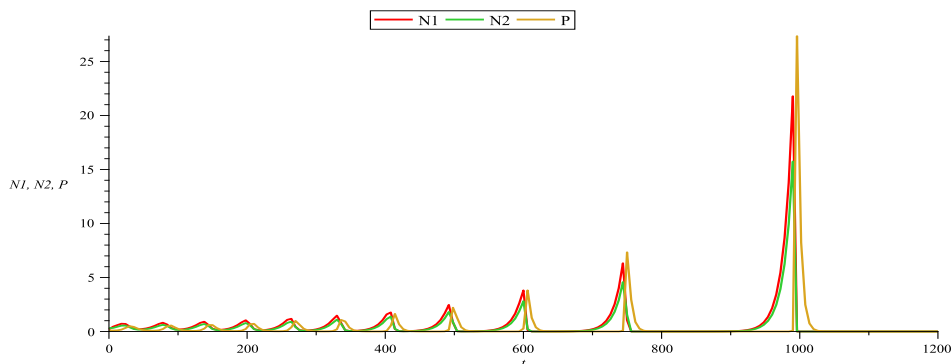

FIGURE 5. Instability of Equilibrium

It is seen in Section 3 that if $b_2g < d_2(d_1 + g)$, then the trivial equilibrium $(0, 0, 0)$ is globally asymptotically stable hence the populations $(N_1(t), N_2(t), P(t))$ remain bounded. Under the assumption (14) that $Dh_1, Dh_2 > 1$ and $b_2g > d_2(d_1 + g)$, we further investigate on the upper bounds of the predator and prey populations in model (1). Referring to the definition of upper-lower solutions in (4), we can define a pair of nonnegative upper-lower solutions $(\tilde{N}_1, \tilde{N}_2, \tilde{P})$ and $(\hat{N}_1, \hat{N}_2, \hat{P})$ for system

(1) satisfying the following differential equations or inequalities:

$$\frac{d\tilde{N}_1}{dt} = b_2\tilde{N}_2 - d_1\tilde{N}_1 - g\tilde{N}_1,$$

$$\frac{d\tilde{N}_2}{dt} = g\tilde{N}_1 - d_2\tilde{N}_2,$$

$$\frac{d\tilde{P}}{dt} \geq \tilde{P}[(e_1s_1\tilde{N}_1 + e_2s_2\tilde{N}_2) * H(e_1s_1h_1\tilde{N}_1 + e_2s_2h_2\tilde{N}_2) - D], \tag{22}$$

$$\tilde{N}_1(0) = N_1(0), \ \tilde{N}_2(0) = N_2(0), \ \tilde{P}(0) = P(0),$$

$$\hat{N}_1(t) = 0, \ \hat{N}_2(t) = 0, \ \hat{P}(t) = 0.$$

From the first two equations in (22), we find the upper solutions for the prey species

$$(\tilde{N}_1(t), \tilde{N}_2(t))^T = e^{At}(N_1(0), N_2(0))^T,$$

with

$$A = \begin{pmatrix} -d_1 - g & b_2 \\ g & -d_2 \end{pmatrix}$$

and

$$e^{At} = \begin{pmatrix} a_{11}e^{\lambda_1 t} + b_{11}e^{\lambda_2 t} & a_{12}e^{\lambda_1 t} + b_{12}e^{\lambda_2 t} \\ a_{21}e^{\lambda_1 t} + b_{21}e^{\lambda_2 t} & a_{22}e^{\lambda_1 t} + b_{22}e^{\lambda_2 t} \end{pmatrix} \tag{23}$$

where $\lambda_1 = -\frac{1}{2}(\alpha+\beta)$ and $\lambda_2 = \frac{1}{2}(\alpha-\beta)$ are eigenvalues of A. For $b_2g > d_2(d_1+g)$,

$$\alpha = \sqrt{(d_1 + d_2 + g)^2 + 4(b_2g - d_1d_2 - d_2g)} > \beta = d_1 + d_2 + g. \tag{24}$$

The coefficients a_{ij} and b_{ij} for e^{At} in (23) are

$$a_{11} = \frac{\alpha + \beta - d_2}{2\alpha} > 0, \ b_{11} = \frac{\alpha - \beta + d_2}{2\alpha} > 0,$$

$$a_{12} = -\frac{b_2}{\alpha} < 0, \ b_{12} = \frac{b_2}{\alpha} > 0,$$

$$a_{21} = -\frac{g}{\alpha} < 0, \ b_{21} = \frac{g}{\alpha} > 0, \tag{25}$$

$$a_{22} = \frac{\alpha + \beta - d_1 - g}{2\alpha} > 0, \ b_{22} = \frac{\alpha - \beta + d_1 + g}{2\alpha} > 0.$$

With $\lambda_1 < 0 < \lambda_2$, the upper solutions $N_1(t)$ and $N_2(t)$ gives upper bounds for the prey populations

$$0 \leq N_1(t) \leq \tilde{N}_1(t) = [a_{11}N_1(0) + a_{12}N_2(0)]e^{\lambda_1 t} + [b_{11}N_1(0) + b_{12}N_2(0)]e^{\lambda_2 t},$$

$$0 \leq N_2(t) \leq \tilde{N}_2(t) = [a_{21}N_1(0) + a_{22}N_2(0)]e^{\lambda_1 t} + [b_{21}N_1(0) + b_{22}N_2(0)]e^{\lambda_2 t} \tag{26}$$

Since each $b_{ij} > 0$ as given in (25) and with $\alpha > d_1 + d_2 + g$ given in (24), one can conclude that for large t:

$$\tilde{N}_1(t) \sim \left[\frac{\alpha - d_1 - g}{2\alpha}N_1(0) + \frac{b_2}{\alpha}N_2(0)\right]e^{\frac{\alpha+d_1+d_2+g}{2}t},$$

$$\hat{N}_2(t) \sim \left[\frac{g}{\alpha}N_1(0) + \frac{\alpha - d_2}{2\alpha}N_2(0)\right]e^{\frac{\alpha+d_1+d_2+g}{2}t}. \tag{27}$$

In order to obtain upper bounds for the predator population, we first note the estimation $0 \leq P(t) \leq \tilde{P}(t) = P(0)e^{\left(\frac{1-D\underline{h}}{\underline{h}}\right)t}$ (where $\underline{h} = \min\{h_1, h_2\}$) given in Section 2. From the assumption $Dh_1, Dh_2 > 1$, we see that $\tilde{P}(t) \to +\infty$ as $t \to \infty$. For an alternate upper bound of the predator population, which depends on more

ecological parameters and the upper bounds for prey populations, we consider the fact

$$\frac{d}{dt}(1 + e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2)$$
$$= [g e_2 s_2 h_2 - (d_1 + g) e_1 s_1 h_1]\tilde{N}_1 + [b_2 e_1 s_1 h_1 - d_2 e_2 s_2 h_2]\tilde{N}_2.$$

Under the assumption for balanced consumption on the prey

$$\frac{d_1 + g}{g} < \frac{e_2 s_2 h_2}{e_1 s_1 h_1} < \frac{b_2}{d_2}, \tag{28}$$

one can obtain the upper solution $\tilde{P}$ for predator population from

$$\frac{d\tilde{P}}{dt} = \tilde{P}\left[k\frac{[g e_2 s_2 h_2 - (d_1 + g)e_1 s_1 h_1]\tilde{N}_1 + [b_2 e_1 s_1 h_1 - b_2 e_2 s_2 h_2]\tilde{N}_2}{1 + e_1 s_1 h_1 \tilde{N}_1 + e_2 s_2 h_2 \tilde{N}_2} - D\right], \tag{29}$$
$$\tilde{P}(0) = P(0),$$

where

$$\frac{1}{k} = \min\{\frac{e_2 s_2 h_h}{e_1 s_1 h_1}g - (d_1 + g), \ \frac{e_1 s_1 h_1}{e_2 s_2 h_h}b_2 - d_2\} > 0. \tag{30}$$

Solving the separable equation (29) leads to the following estimation

$$0 \leq P(t) \leq \tilde{P}(t) = P(0)\left[\frac{1 + e_1 s_1 h_1 \tilde{N}_1(t) + e_2 s_2 h_2 \tilde{N}_2(t)}{1 + e_1 s_1 h_1 N_1(0) + e_2 s_2 h_2 N_2(0)}\right]^k e^{-Dt}. \tag{31}$$

For large t, the upper bound for the predator population

$$\tilde{P}(t) \sim P(0)e^{(k\lambda_2 - D)t}. \tag{32}$$

6. **Discussion/conclusion.** In this paper, we work on mathematical analysis of the predator-prey model (1) with a stage-structured prey, which was initially presented and studied in [1]. This model has three possible types of equilibrium points: $(0, 0, 0)$, $(N_1, N_2, 0)$, and $(\overline{N}_1, \overline{N}_2, \overline{P})$, representing different ecological outcomes.

The global asymptotic stability of the trivial equilibrium is ensured by the condition $b_2 g < d_2(d_1 + g)$ (Theorem 3.1). Both the predator and prey will go to extinction if the difference between the birth-to-death ratio b_2/d_2 of the adult prey and the death-to-transition ratio d_1/g of the juvenile prey is less than 1. When the difference is exactly 1, the system has infinitely many prey-only equilibria $(N_1, N_2, 0)$ with adult-to-juvenile ratio as g/d_2, so there is no asymptotic stability. The condition in Theorem 3.2 implies that each of the prey-only equilibrium is unstable the death rate D of the predator is sufficiently small or the capture rate (s_i) and relative nutritional value (e_i) of prey are sufficiently large.

The main focus of the analysis in this paper is to examine the possibility for long-term survival of both the prey and predator while the difference between the ratios b_2/d_2 and d_1/g is larger than 1 and the product of predator death rate and handling time $Dh_i < 1$. We first study the coexistence equilibrium in two special cases where only one stage (adult or juvenile) of the prey is vulnerable. It is seen that the equilibrium values of the species in (6) and (11) depend on all ecological parameters, but the stability conditions (in Theorem 4.1 and Theorem 4.2) are not affected by the capture rate s_i and relative nutritional value e_i of the prey. The prey and predator can coexist when the death rate of adult prey d_2 or the sum of juvenile prey death rate and transition rate $d_1 + g$ is small enough. These conclusions are similar to the results in [1], under some simplified condition for parameters.

Most importantly, when adult and juvenile prey are both vulnerable, we investigate the presence and asymptotic stability of a unique coexistence equilibrium as well as the dynamic behavior of all species. We find (for the first time) the exact values of the unique coexistence equilibrium and conditions for its (local) asymptotic stability or instability. These results are made possible by the discovery of the adult-to-juvenile ratio $r > (d_1 + g)/b_2$ given in (17), which also indicate that for coexistence the adult prey needs to be relatively sizable comparing to the juvenile prey. The stability condition of the coexistence equilibrium obtained in Theorem 5.1 is demonstrated through simulations in Fig. 4. When that condition fails, we observe in Fig. 5 a different type of dynamics for long-term survival of all the species with a pattern of oscillation with increasing magnitude. The complexity of the model is demonstrated in both the stability analysis through linearization (Theorem 5.2) and the estimations of upper bounds for all populations. Each of the ecological parameters (including s_i and e_i) plays its unique role in the dynamics (equilibrium values, stability, and upper bounds) of the model, and should not be ignored.

REFERENCES

[1] P. A. Abrams and C. Quince, The impact of mortality rate on predator population size and stability in systems with stage-structured prey, *Theoretical Population Biology,* **68** (2005), 253–266.

[2] B. Buonomo, D. Lacitignola and S. Rionero, Effect of prey growth and predator cannibalism rate on the stability of a structured population model, *Nonlinear Analysis: Real World Applications,* **11** (2010), 1170–1181.

[3] L. Cai and X. Song, Permanence and stability of a predator-prey system with stage structure for predator, *Journal of Computational and Applied Mathematics,* **201** (2007), 356–366.

[4] R. S. Cantrell and C. Cosner, Permanence in ecological systems with spatial heterogeneity, *Proc. Roy. Soc. Edinburgh,* **123** (1993), 533–559.

[5] F. Chen, Permanence of periodic Holling type predator-prey system with stage structure for prey, *Applied Mathematics and Computation,* **182** (2006), 1849–1860.

[6] D. Cooke and J. A. Leon, Stability of population growth determined by 2x2 Leslie Matrix with density dependent elements, *Biometrics,* **32** (1976), 435–442.

[7] J. M. Cushing and M. Saleem, A predator prey model with age structure, *Journal of Mathematical Biology,* **14** (1982), 231–250.

[8] M. Fan and Y. Kuang, Dynamics of a nonautonomous predator-prey system with the Beddington-DeAngelis functional response, *J. Math. Anal. Appl.,* **295** (2004), 15–39.

[9] W. Feng, Coexistence, stability, and limiting behavior in a one-predator-two-prey model, *J. Math. Anal. Appl.,* **179** (1993), 592–609.

[10] W. Feng, Permanence effect in a three-species food chain model, *Applicable Analysis,* **54** (1994), 195–209.

[11] W. Feng and X. Lu, Harmless delays for permanence in a class of population models with diffusion effects, *J. Math. Anal. Appl.,* **206** (1997), 547–566.

[12] W. Feng and X. Lu, Some coexistence and extinction results in a three species ecological model, *Diff. Integ. Eq.s,* **8** (1995), 617–626.

[13] W. Feng, C. V. Pao and X. Lu, Global attractors of reaction-diffusion systems modeling food chain populations with delays, *Commun. Pure Appl. Anal.,* **10** (2011), 1463–1478.

[14] A. Hastings, Age-dependent predation is not a simple process, I: Continuous time models, *Theorertical Population Biology,* **23** (1983), 347–362.

[15] A. Leung, Limiting behaviour for a prey-predator model with diffusion and crowding effects, *J. Math. Biol.,* **6** (1978), 87–93.

[16] B. C. Longstaff, The dynamics of collembolan population growth, *Canadian Journal of Zoology,* **55** (1977), 314–324.

[17] C. Lu, W. Feng and X. Lu, Long-term survival in a 3-species ecological system, *Dynam. Contin. Discrete Impuls. Systems,* **3** (1997), 199–213.

[18] G. A. Oster, Internal variables in population dynamics, In *Levin, S.A. (Ed.), Lectures on Mathematics in the Life Sciences*, **8** (1976), American Mathematical Society, Providence, RI, 37–68.

[19] C. V. Pao, *Nonlinear Parabolic and Elliptic Equations*, Plenum Press, N.Y., 1992.

[20] R. H. Smith and R. Mead, Age structure and stability in models of prey-predator systems, *Theoretical Population Biology,* **6** (1974), 308–322.

[21] C. Sun, Y. Lin and M. Han, Dynamic analysis for a stage-structure competitive system with mature population harvesting, *Chaos, Solitons & Fractals,* **31** (2007), 380–390.

[22] H. Wang, J. D. Nagy, O. Gilg and Y. Kuang, The roles of predator maturation delay and functional response in determining the periodicity of predator-prey cycles, *Mathematical Biosciences,* **221** (2009), 1–10.

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