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Rich dynamics of a ratio-dependent one-prey two-predators model

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Abstract. The objective of this paper is to systematically study the qualitative properties of a ratio-dependent one-prey two-predator model. We show that the dynamics outcome of the interactions are very sensitive to parameter values and initial data. Specifically, we show the interactions can lead to all the following possible outcomes: 1) competitive exclusion; 2) total extinction, i.e., collapse of the whole system; 3) coexistence in the form of positive steady state; 4) coexistence in the form of oscillatory solutions; and 5) introducing a friendly and better competitor can save a otherwise doomed prey species. These results reveal far richer dynamics compared to similar prey dependent models. Biological implications of these results are discussed.

1. Introduction

Generally, a **predator-dependent** predator-prey model takes the form

$$\begin{cases} x' = xg(x/K) - yP(x, y), & x(0) > 0, \\ y' = cyP(x, y) - dy, & y(0) > 0. \end{cases} \quad (1.1)$$

When $P(x, y) = p(x/y)$, we call model (1.1) (strictly)**ratio-dependent**. The traditional (or **prey-dependent**) model takes the form

$$\begin{cases} x' = xg(x/K) - yp(x), & x(0) > 0, \\ y' = cyp(x) - dy, & y(0) > 0 \end{cases} \quad (1.2)$$

Mathematically, we may think both the traditional prey-dependent and ratio-dependent models as limiting cases ($c = 0$ for the former and $a = 0$ for the latter) of the general Beddington-DeAngelis type predator-dependent functional response

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$P(x, y) = \alpha x/(a+bx+cy)$ or the or Hassell-Varley type $P(x, y) = P(x/y^\gamma)$, $\gamma \in [0, 1]$. (Beddington(1975), DeAngelis et al.(1975), Hassell and Varley(1969)). This view is also plausible biologically (Cosner et al.(1999)).

When $p(x) = \alpha x/(m+x)$ and $g(x/K) = r(1-x/K)$, model (1.2) becomes the following well studied Michaelis-Menten type predator-prey system (see the references cited in Kuang and Freedman(1988)).

$$\begin{cases} x' = rx(1-x/K) - \alpha xy/(m+x), & x(0) > 0, \\ y' = y(-d + fx/(m+x)), & y(0) > 0 \end{cases} \quad (1.3)$$

where r, K, α, m, f, d are positive constants and $x(t), y(t)$ represent the population density of prey and predator at time t respectively. The prey grows with intrinsic growth rate r and carrying capacity K in the absence of predation. The predator consumes the prey with functional response of Michaelis-Menten type $cx y/(m+x)$ and contributes to its growth with rate $fx y/(m+x)$. The constant d is the death rate of predator. This model exhibits the well-known “paradox of enrichment” observed by Hairston et al.(1960) and by Rosenzweig(1969) which states that according to model (1.3), enriching a predator-prey system (increasing the carrying capacity K) will cause an increase in the equilibrium density of the predator but not in that of the prey, and will destabilize the positive equilibrium (the positive steady state changes from stable to unstable as K increases). An equivalent paradox is the so called “biological control paradox” which was recently brought into discussion by Luck (1990), stating that according to (1.3), we cannot have both a low and stable prey equilibrium density. However, in reality, there are numerous examples of successful biological control where the prey are maintained at densities less than 2% of their carrying capacities (Arditi and Berryman (1991)). This clearly indicates that the paradox of biological control is not intrinsic to predator-prey interactions. Another noteworthy prediction from model (1.3) is that prey and predator species can not extinct simultaneously (mutual extinction). This, however, contradicts Gause’s classic observation of mutual extinction in the protozoans, *Paramecium* and its predator *Didinium* (Gause(1934), Luckinbill(1973), Abrams and Ginzburg(2000)), and the well cited experimental observation of Huffaker (Huffaker(1958)).

Until very recently, both ecologists and mathematicians chose to ignore the rich dynamics provided by the strict ratio-dependent models, especially that on the boundary and close to the origin (the origin is a singular equilibrium, which renders direct local stability analysis impossible). Some researchers regard such interesting dynamics as “pathological behavior”. However, some empirical and theoretical evidence (e.g., Akcakaya et al.(1995, Ecology)) suggests that such “pathological behavior” is not only realistic, but the lack of such dynamics in prey-predator models actually makes them pathological in a biological sense. Recent efforts (Kuang and Beretta(1998), Kuang(1999), Jost et al.(1999)) show that the presupposed “pathological behavior” of solutions are not pathological at all. To see this point more clearly, consider the following example of “pathological behavior”. For ratio-dependent model, even if there is a positive steady state, both prey and predator can still go extinct (Kuang(1999)). The extinction (i.e., the collapse of the system) may occur in two distinct ways. One of the way is both species become extinct regardless of the initial densities, such as the Gause’s classic observation of mutual

extinction in the protozoans, *Paramecium* and its predator *Didinium* (Gause(1934), Abrams and Ginzburg(2000)). The other way is both species will die out only if the initial prey/predator ratio is too low. In the first case, extinction often occur as a result of high predator efficiency in catching and/or converting prey biomass). The second way has some subtle and interesting implications. For example, it indicates that altering the ratio of prey to predators through over-harvesting of prey species, or over-stocking of predators may lead to the collapse of the whole system and the extinction of both species.

It turns out that, in many aspects, the ratio-dependent models actually provide the richest dynamics, while the prey-dependent ones provide the least in dynamical behavior (Kuang and Beretta(1998), Jost et al.(1999), Hsu et al.(2001) and Berezovskaya et al.(2001)). Since the ratio-dependent form use one less parameter than the Beddington-DeAngelis one, it is thus more appealing for both analytical and experimental applications (Jost and Arditi(2000)).

During the period of between late eighties and late nineties, there is a much heated debate on the validity of the ratio-dependent based population models(Abrams(1994, 1997), Abrams and Ginzburg(2000)) and there are still some legitimately controversial aspects of ratio-dependence (such controversies can be found in Abrams and Ginzburg(2000)). A specific main controversial aspect is that well documented mechanistic justification of the ratio-dependent model (Cosner et al. (1999)) requires high population densities of both prey and predator species while most interesting dynamics of ratio-dependent models occurs near the origin. This is certainly a valid concern if the area of the population interaction is large (Arditi and Ginzburg (1989), Cosner et al. (1999)), Abrams and Ginzburg (2000)), since in such case, predators will spend most effort in searching rather than interfering each other. Hence, the functional response is likely to be much more sensible to prey density than predator density. However, if the habitat is small and free of refugees for prey, then arguably, ratio dependence formulation may remain valid even when densities are low, since predators can remain effectively interfering each other. For very small patch or field, even when the numbers of individuals of prey and predators are low, their densities may remain high. In such case, ratio-dependence can be a valid model mechanism which suggests that mutual extinction is highly possible. This provides a simple and plausible explanation for Gause's classic observation of mutual and deterministic extinction in the protozoans, *Paramecium* and its predator *Didinium* (Abrams and Ginzburg (2000)). Indeed, deterministic extinction of both species is, while an extreme outcome of the predator-prey interaction in the field, is becoming ever more frequent and worrisome. The public believes this resulted from the fragmentation of habitats and the ever shrinking sizes of these patches which may diminish or deprive of prey refugees (Fischer (2000)). Ratio dependence, while a special case of the general predator dependence ones (Beddington-DeAngelis or Hassell-Varley type (Cosner et al.(1999)), is currently the only one that provides a simple and plausible support to such public view in addition to providing a plausible explanation of the success of biological controls (Ebert et al.(2000)).

The following Michaelis-Menten type ratio-dependent predator-prey system was studied extensively (Kuang and Beretta(1998), Jost et al.(1999), Hsu et al.(2001),

Berezovskaya et al.(2001), and the references cited))

$$\begin{cases} x' = rx(1 - x/K) - \alpha xy/(my + x), & x(0) > 0, \\ y' = y(-d + fx/(my + x)), & y(0) > 0 \end{cases} \tag{1.4}$$

where r, K, α, m, f, d are positive constants and $x(t), y(t)$ represent the population density of prey and predator at time t respectively. The prey grows with intrinsic growth rate r and carrying capacity K in the absence of predation. The predator consumes the prey with functional response of Michaelis-Menten type $cxy/(my + x)$ and contributes to its growth with rate $fx y/(my + x)$. The constant d is the death rate of predator. It is straightforward to generalize the above two species model to the situation when one prey species shared by two competing predator species. This results in the following three species strict ratio-dependent predator-prey model

$$\begin{cases} x' = rx(1 - \frac{x}{K}) - \frac{c_1xy_1}{a_1x + y_1 + my_2} - \frac{c_2xmy_2}{a_2x + y_1 + my_2} \\ y'_1 = y_1(-d_1 + \frac{e_1c_1x}{a_1x + y_1 + my_2}) \\ y'_2 = y_2(-d_2 + \frac{e_2c_2mx}{a_2x + y_1 + my_2}). \end{cases} \tag{1.5}$$

Here the meanings of r, K are obvious and c_1, c_2 are searching efficiency constants. m is the relative predation rate of y_2 with respect to y_1 . $c_1/a_1, c_2m/a_2$ describes the maximum per-capita capturing rate for y_1, y_2 respectively. e_1, e_2 are conversion rates and d_1, d_2 are death rates. This model can also be formally derived from the general multi-species ratio-dependent model construction procedures proposed in Arditi and Michalski(1996).

Our analysis on this ratio-dependent one prey-two predators model reveals many new and interesting dynamics. While competitive exclusion principle still hold for most parameter values for the competing predators, it is very often that we see both can go extinct as either the result of the parameter values or the selection of initial data. In fact, for certain choices of parameters and initial values, even the prey species can go extinct, which in turn cause the extinction of both predators. Still, for some parameter values, coexistence is possible in both the forms of positive steady state and oscillatory solutions. Most surprisingly, we show that when a predator is capable of driving the prey and itself to extinction, the introduction of a predator which is more friendly (to prey) and is a stronger (compared to the existing one) competitor may save the prey species.

2. The preliminary results

It is convenient to scale the variables. Let $\bar{x} = x/K, \bar{y}_1 = y_1, \bar{y}_2 = my_2, \bar{c}_1 = c_1, \bar{c}_2 = c_2, \bar{a}_1 = a_1K, \bar{a}_2 = a_2K, \bar{e}_1 = e_1K, \bar{e}_2 = e_2Km$. Making these changes and dropping the bars from the resulting equations yields the following system

without K and m .

$$\begin{cases} x' = rx(1 - x) - \frac{c_1xy_1}{a_1x + y_1 + y_2} - \frac{c_2xy_2}{a_2x + y_1 + y_2} = X(x, y_1, y_2) \\ y_1' = y_1(-d_1 + \frac{e_1c_1x}{a_1x + y_1 + y_2}) = Y_1(x, y_1, y_2) \\ y_2' = y_2(-d_2 + \frac{e_2c_2x}{a_2x + y_1 + y_2}) = Y_2(x, y_1, y_2) \end{cases} \tag{2.1}$$

We consider only the biologically meaningful initial condition

$$x(0) \geq 0, \quad y_1(0) \geq 0, \quad y_2(0) \geq 0.$$

Due to the boundedness of the functional responses, we see that

$$\begin{aligned} \lim_{(x,y_1,y_2) \rightarrow (0,0,0)} X(x, y_1, y_2) &= \lim_{(x,y_1,y_2) \rightarrow (0,0,0)} Y_1(x, y_1, y_2) \\ &= \lim_{(x,y_1,y_2) \rightarrow (0,0,0)} Y_2(x, y_1, y_2) = 0. \end{aligned}$$

Hence, if we let $X(0, 0, 0) = Y_1(0, 0, 0) = Y_2(0, 0, 0) = 0$, then these function are continuous on $R_+^3 = \{(x, y_1, y_2) : x \geq 0, y_1 \geq 0, y_2 \geq 0\}$. Indeed, straightforward computation shows that they are Lipschitzian on R_+^3 . Hence solution of (2.1) with nonnegative initial condition exists and is unique. It is also easy to see that these solutions exist for all $t > 0$ and stay nonnegative. In fact, if $x(0) > 0$, then $x(t) > 0$ for all $t > 0$. Same is true for y_1 and y_2 components. Hence, the interior of R_+^3 is invariant for model (2.1).

Observe that

$$x' \leq rx(1 - x),$$

which implies that

$$\limsup_{t \rightarrow \infty} x(t) \leq 1.$$

This implies that for any $0 < \varepsilon < 1$, we have $x(t) < 1 + \varepsilon$ for large t . Let

$$d = \min\{d_1, d_2\}.$$

We have

$$\begin{aligned} x' + y_1'/e_1 + y_2'/e_2 &= rx(1 - x) - (d_1/e_1)y_1 - (d_2/e_2)y_2 \\ &\leq (r + d)x - d(x + y_1/e_1 + y_2/e_2). \end{aligned}$$

This leads to

$$\limsup_{t \rightarrow \infty} (x(t) + y_1(t)/e_1 + y_2(t)/e_2) \leq (r + d)/d. \tag{2.2}$$

Hence we have shown that model (2.1) is dissipative. It is also straightforward to show that the first and second derivatives of x, y_1, y_2 are all continuous and bounded.

3. Competitive exclusion: extinction of at least one predator

Observe that if $e_1c_1 \leq a_1d_1$, then for positive solutions,

$$y'_1 = -y_1((a_1d_1 - e_1c_1)x + d_1y_1 + d_1y_2)/(a_1x + y_1 + y_2) < 0.$$

Clearly $y_1(t)$ is strictly decreasing and hence it must tend to a nonnegative constant, say y_{10} . Since the model is dissipative, we have a positive constant, say M , such that for large time, say for $t > t_0 > 0$, $a_1x + y_1 + y_2 < M$. If $y_{10} \neq 0$, then there is a $t_1 > t_0$, such that for $t > t_1$, we have $y_1(t) > y_{10}/2$. Hence, for $t > t_1$, we have

$$y'_1 < -\frac{d_1y_{10}}{2M}y_1$$

which implies that $\lim_{t \rightarrow \infty} y_1(t) = 0 \neq y_{10}$. This contradiction shows that we must have $y_{10} = 0$. Similar statement can be made for the y_2 species. We summarize the above argument as the following theorem.

Lemma 3.1. *Consider (2.1). If $e_1c_1 \leq a_1d_1$, then $\lim_{t \rightarrow \infty} y_1(t) = 0$. If $e_2c_2 \leq a_2d_2$, then $\lim_{t \rightarrow \infty} y_2(t) = 0$.*

The next theorem is the result of the application of a comparison argument.

Theorem 3.1. *If $a_2 \geq a_1$ and*

$$\frac{e_1c_1}{d_1} - a_1 > \frac{e_2c_2}{d_2} - a_2 > 0, \tag{3.1}$$

in (2.1), then $\lim_{t \rightarrow \infty} y_2(t) = 0$.

Proof. We assume that (3.1) holds true. Let $z = y_1 + y_2$ and $\theta > 0$ to be determined. We have

$$\theta \frac{y'_2}{y_2} - \frac{y'_1}{y_1} = \frac{P(x, z)}{(a_1x + z)(a_2x + z)}$$

where

$$\begin{aligned} P(x, z) &= \theta(a_1x + z)((e_2c_2 - a_2d_2)x - d_2z) - (a_2x + z)((e_1c_1 - a_1d_1)x - d_1z) \\ &= [a_1\theta(e_2c_2 - a_2d_2) - a_2(e_1c_1 - a_1d_1)]x^2 + (d_1 - d_2\theta)z^2 \\ &\quad + [\theta(e_2c_2 - a_2d_2 - a_1d_2) - (e_1c_1 - a_1d_1 - a_2d_1)]xz \\ &= A(\theta)x^2 + B(\theta)xz + C(\theta)z^2. \end{aligned} \tag{3.2}$$

The discriminant of (3.2) is

$$\begin{aligned} \Delta(\theta) &= [\theta(e_2c_2 - a_2d_2 - a_1d_2) - (e_1c_1 - a_1d_1 - a_2d_1)]^2 - 4[a_1\theta(e_2c_2 - a_2d_2) \\ &\quad - a_2(e_1c_1 - a_1d_1)](d_1 - d_2\theta) \\ &= \theta^2(e_2c_2 - a_2d_2 - a_1d_2)^2 + (e_1c_1 - a_1d_1 - a_2d_1)^2 \\ &\quad - 2\theta(e_2c_2 - a_2d_2 - a_1d_2)(e_1c_1 - a_1d_1 - a_2d_1) + 4a_1d_2(e_2c_2 - a_2d_2)\theta^2 \\ &\quad - 4\theta[a_1d_1(e_2c_2 - a_2d_2) + a_2d_2(e_1c_1 - a_1d_1)] + 4a_2d_1(e_1c_1 - a_1d_1) \\ &= \theta^2((e_2c_2 - a_2d_2) + a_1d_2)^2 + ((e_1c_1 - a_1d_1) + a_2d_1)^2 \end{aligned}$$

$$\begin{aligned}
 & -2\theta[(e_2c_2 - a_2d_2) - a_1d_2][(e_1c_1 - a_1d_1) - a_2d_1] \\
 & + 2a_1d_1(e_2c_2 - a_2d_2) + 2a_2d_2(e_1c_1 - a_1d_1)] \\
 = & [\theta(e_2c_2 - a_2d_2 + a_1d_2) - ((e_1c_1 - a_1d_1 + a_2d_1))^2 \\
 & - 2\theta[-2a_2d_1(e_2c_2 - a_2d_2) \\
 & - 2a_1d_2(e_1c_1 - a_1d_1) + 2a_1d_1(e_2c_2 - a_2d_2) + 2a_2d_2(e_1c_1 - a_1d_1)] \\
 = & [\theta(e_2c_2 - a_2d_2 + a_1d_2) - ((e_1c_1 - a_1d_1 + a_2d_1))^2 \\
 & + 4\theta(a_1 - a_2)d_1d_2[(\frac{e_1c_1}{d_1} - a_1) - (\frac{e_2c_2}{d_2} - a_2)].
 \end{aligned}$$

We chose

$$\theta = \theta^* = \frac{e_1c_1 - a_1d_1 + a_2d_1}{e_2c_2 - a_2d_2 + a_1d_2} > 0.$$

Then, from (3.1) and the fact that $a_2 \geq a_1$, we see that

$$\Delta(\theta^*) = 4\theta^*(a_1 - a_2)d_1d_2[(\frac{e_1c_1}{d_1} - a_1) - (\frac{e_2c_2}{d_2} - a_2)] \leq 0.$$

Notice that $\Delta(\theta^*) = 0$ if and only if $a_1 = a_2$.

We now would like to determine the signs of the coefficients of x^2 and z^2 in (3.2). For the coefficient of x^2 , we have

$$\begin{aligned}
 A(\theta^*) & = a_1\theta^*(e_2c_2 - a_2d_2) - a_2(e_1c_1 - a_1d_1) \\
 & = \frac{1}{e_2c_2 - a_2d_2 + a_1d_2} [a_1(e_2c_2 - a_2d_2)(e_1c_1 - a_1d_1 + a_2d_1) \\
 & \quad - a_2(e_2c_2 - a_2d_2 + a_1d_2)(e_1c_1 - a_1d_1)] \\
 & = \frac{1}{e_2c_2 - a_2d_2 + a_1d_2} [(a_1 - a_2)(e_1c_1 - a_1d_1)(e_2c_2 - a_2d_2) \\
 & \quad - a_1a_2d_1d_2[(\frac{e_1c_1}{d_1} - a_1) - (\frac{e_2c_2}{d_2} - a_2)] < 0.
 \end{aligned}$$

For the coefficient of z^2 , we have

$$C(\theta^*) = d_1 - d_2\theta^* = \frac{-d_1d_2}{e_2c_2 - a_2d_2 + a_1d_2} [(\frac{e_1c_1}{d_1} - a_1) - (\frac{e_2c_2}{d_2} - a_2) + a_2 - a_1] < 0.$$

Therefore $P(x, z) \leq 0$. Since $\Delta(\theta^*) = 0$ if and only if $a_1 = a_2$, in which case we have the coefficient of xz

$$\begin{aligned}
 B(\theta^*) & = \theta^*(e_2c_2 - a_2d_2 - a_1d_2) - (e_1c_1 - a_1d_1 - a_2d_1) \\
 & = \frac{2}{e_2c_2 - a_2d_2 + a_1d_2} [a_2d_1(e_2c_2 - a_2d_2) - a_1d_2(e_1c_1 - a_1d_1)] \\
 & = \frac{2}{e_2c_2 - a_2d_2 + a_1d_2} a_1d_1d_2(e_2c_2/d_2 - e_1c_1/d_1) < 0.
 \end{aligned}$$

Hence, $P(x, z) = 0$ if and only if one of the following is true:

- i): $\Delta(\theta^*) < 0$ and hence $x = z = 0$;
- ii): $\Delta(\theta^*) = 0$ and hence $a_1 = a_2$ and $(-A(\theta^*))^{1/2}x = -(-C(\theta^*))^{1/2}z$.

Since $x \geq 0, z \geq 0$, we see that (ii) also leads to $x = z = 0$. Clearly, $z = 0$ implies that $y_1 = y_2 = 0$. In summary, we have shown that

$$P(x, z) = 0 \text{ implies that } x = y_1 = y_2 = 0. \tag{3.3}$$

Consider now a Liapunov function of the form

$$V = V(x, y_1, y_2) = \frac{y_2^{\theta^*}}{y_1}.$$

Then

$$dV/dt = V \frac{P(x, z)}{(a_1x + z)(a_2x + z)} \leq 0.$$

$dV/dt = 0$ if and only if $y_2 = 0$ or $P(x, z) = 0$. Since $P(x, z) = 0$ also implies that $y_2 = 0$, we thus have $dV/dt = 0$ if and only if $y_2 = 0$. The standard Liapunov-LaSalle theorem implies that

$$\lim_{t \rightarrow \infty} y_2(t) = 0.$$

This proves the theorem. □

Observe that when $y'_i = 0$, we have

$$x = \frac{y_1 + y_2}{e_i c_i / d_i - a_i}, \quad i = 1, 2.$$

Hence, (3.1) simply states that predator 1 has a lower break-even prey density requirement than predator 2. In the rest of this paper, we say predator i is a *stronger predator* than predator j , if $i \neq j$, and

$$a_j \geq a_i \quad \text{and} \quad \frac{e_i c_i}{d_i} - a_i > \frac{e_j c_j}{d_j} - a_j > 0. \tag{3.4}$$

To conclude this section, we point out that in order to have $(x, y_1, y_2) \rightarrow (x^*, y_1^*, 0)$, it is necessary to have

$$e_1 c_1 / d_1 - a_1 \geq e_2 c_2 / d_2 - a_2.$$

This suggests that Theorem 3.1 is reasonably sharp. To see this, suppose $(x, y_1, y_2) \rightarrow (x^*, y_1^*, 0)$. Then

$$d_1 = (e_1 c_1 x^*) / (a_1 x^* + y_1^*)$$

and

$$d_2 \geq (e_2 c_2 x^*) / (a_2 x^* + y_1^*)$$

Then

$$d_1 / (e_1 c_1) = x^* / (a_1 x^* + y_1^*)$$

and

$$d_2 / (e_2 c_2) \geq x^* / (a_2 x^* + y_1^*)$$

Hence

$$e_1 c_1 / d_1 - a_1 = y_1^* / x^* \geq e_2 c_2 / d_2 - a_2.$$

4. System saver

We say a predator is a *system destroyer* if left alone with a prey population, it drives both itself and the prey to extinction (forming a collapsing predator-prey interaction). For example, according to Theorem 2.6 of Kuang and Beretta(1998), if

$$e_i c_i / a_i > d_i c_i / (c_i - r), \quad c_i > r, \quad i = 1, 2,$$

then predator i is a system destroyer. We say a predator is a *system saver* if its introduction to a collapsing predator-prey system can prevent the prey from going extinct. The main objective of this section is to show that system savers do exist.

Theorem 4.1. *If $a_2 \leq \min\{a_1, e_2\}$ and*

$$e_1 c_1 / a_1 > d_1 c_1 / (c_1 - r), \quad c_1 > r, \tag{4.1}$$

$$\frac{e_2 c_2}{d_2} - a_2 > \frac{e_1 c_1}{d_1} - a_1 > 0, \tag{4.2}$$

$$x^* = 1 - \frac{c_2}{r} \left(1 - \frac{a_2 d_2}{e_2 c_2}\right) > 0, \tag{4.3}$$

in (2.1), then the boundary steady state $E_2 := (x^*, 0, y_2^*)$, where $y_2^* = (e_2 c_2 / d_2 - a_2) x^*$, is locally asymptotically stable. Therefore, predator 2 is a system saver.

Proof. Direct computation shows that the variational matrix at E_2 is $A = (a_{ij})_{3 \times 3}$, where

$$\begin{aligned} a_{11} &= x^* (-r + c_2 a_2 y_2^* \Delta^{-2}), \\ a_{13} &= -c_2 a_2 (x^*)^2 \Delta^{-2}, \\ a_{21} &= a_{23} = 0, \\ a_{22} &= -d_1 + e_1 c_1 x^* \Delta^{-1} = d_1 [(e_1 c_1 / d_1 - a_1) x^* - y_2^*] \Delta^{-1} < 0, \\ a_{31} &= e_2 c_2 (y_2^* / \Delta)^2, \\ a_{33} &= e_2 c_2 x^* y_2^* \Delta^{-2} \\ \Delta &= a_2 x^* + y_2^* = e_2 c_2 x^* / d_2. \end{aligned}$$

Since $a_{21} = a_{23} = 0$, we see that to determine the local asymptotical stability of E_2 , it is sufficient to study that of

$$A_{22} = \begin{bmatrix} a_{11} & a_{13} \\ a_{31} & a_{33} \end{bmatrix}. \tag{4.4}$$

We have

$$\begin{aligned} \det(A_{22}) &= r e_2 c_2 (x^*)^2 y_2^* / \Delta^{-2} > 0 \\ \text{tr}(A_{22}) &= -r x^* + c_2 x^* y_2^* (a_2 - e_2) \Delta^{-2} < 0. \end{aligned}$$

This together with $a_{22} < 0$ imply that E_2 is locally asymptotically stable. □

It is obvious that the above theorem remains true if we replace the simple condition of $a_2 \leq e_2$ by the sharper but more complicated one of $\text{tr}(A_{22}) = -r x^* +$

$c_2x^*y_2^*(a_2 - e_2)\Delta^{-2} < 0$. Condition (4.3) simply ensures that prey species can coexist with predator 2 alone.

Figure 1 illustrates an example where predator 1 is a destroyer and Figure 2 shows that for this destroyer, predator 2 is a system saver. Here $a_1 = a_2 = d_1 = d_2 = 1, c_1 = 2.800, c_2 = 1.800, e_1 = 0.536, e_2 = 1$. For this set of parameters, solutions are very sensitive to initial population values. If initial value of predator 1 is too large, or initial value of prey is too small, total extinction is the outcome.

5. Total extinction

In this section, we consider the possibility of total extinction in model (2.1). This can happen through many ways. For an example, the addition of a system destroyer which is also a stronger competitor will eliminate the competitor and the prey species, leading to total extinction of the system. This is simply the result of our Theorem 3.1 and Theorem 2.6 of Kuang and Beretta(1998). Explicit conditions in term of model parameters for this to happen can be easily obtained. This forms the following theorem.

Theorem 5.1. *If $a_2 \geq a_1$ and*

$$e_1c_1/a_1 > d_1c_1/(c_1 - r), \quad c_1 > r, \tag{5.1}$$

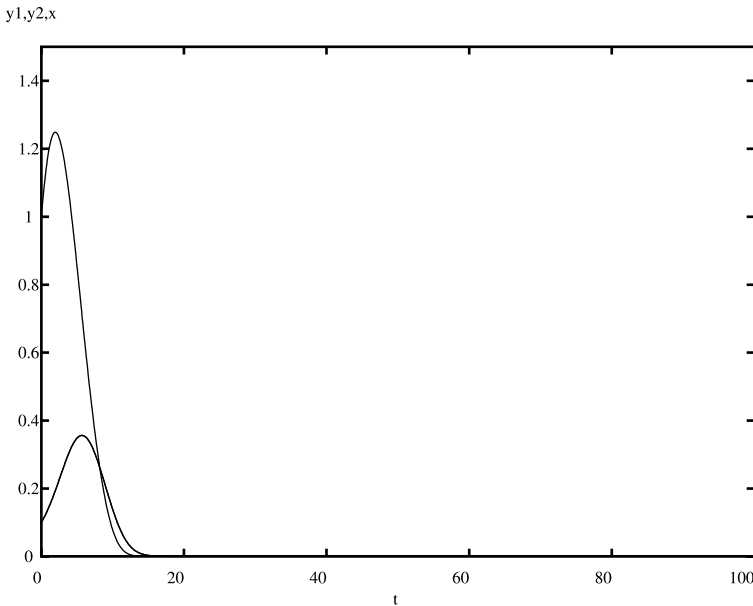


Fig. 1. This figure shows the solution of (2.1) when $r = 1, a_1 = a_2 = d_1 = d_2 = 1, c_1 = 2.800, c_2 = 1.800, e_1 = 0.536, e_2 = 1, x(0) = 1, y_1(0) = 0.1, y_2(0) = 0$. The top curve (at the beginning) depicts prey species and the bottom curve (at the beginning) depicts predator 1. Clearly, predator 1 is a destroyer.

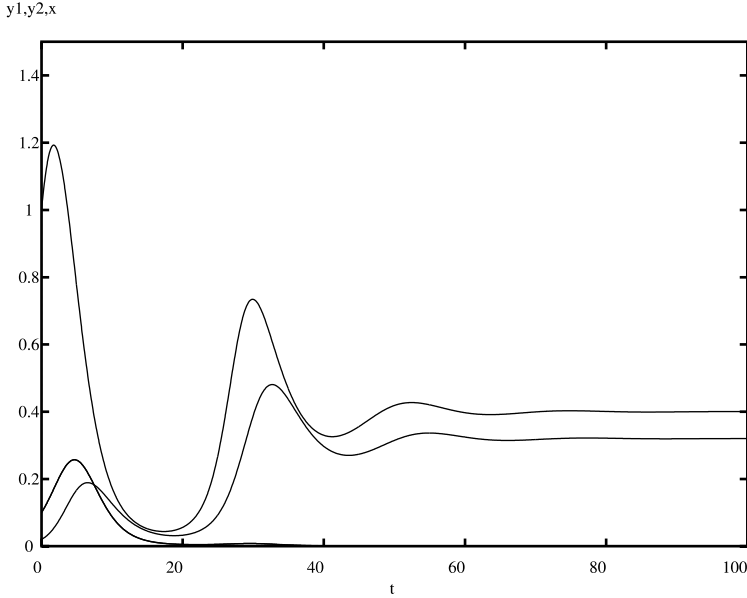


Fig. 2. This figure shows the solution of (2.1) when $r = 1, a_1 = a_2 = d_1 = d_2 = 1, c_1 = 2.800, c_2 = 1.800, e_1 = 0.536, e_2 = 1, x(0) = 1, y_1(0) = 0.1, y_2(0) = 0.01$. The top curve (at the beginning) depicts prey species and the bottom curve (at the beginning) depicts predator 2. We see that predator 2 is a system saver.

$$\frac{e_1 c_1}{d_1} - a_1 > \frac{e_2 c_2}{d_2} - a_2 > 0, \tag{5.2}$$

in (2.1), then the origin is globally attractive.

Proof. From Theorem 3.1, we see that $a_2 \geq a_1$ and (5.2) together imply that $\lim_{t \rightarrow \infty} y_2(t) = 0$. Let

$$m_1 = e_1 c_1, \quad m_2 = e_2 c_2, \quad u = x / (y_1 + y_2).$$

Then (2.1) can be transformed to (6.2). The limiting system when $y_2 = 0$ takes the form of (6.4) which has no degenerate steady states. A simple flow analysis of (6.2) (similar to the one performed in Kuang and Beretta(1998) for the proof of their Theorem 2.6) shows that the origin in (6.4) is globally asymptotically stable with respect to positive solutions under the condition of (5.1). The Theorem 1.6 of Thieme(1992) (see also Thieme(1994)) implies that positive solutions of (2.1) must also tend to the origin. This complete the proof. \square

The above theorem illustrates that total extinction is a direct result of the local or global stability of the origin. The following theorem provides another set of sufficient conditions for the global stability of the origin. Biologically, this theorem, like the previous one, provide a recipe for the eventual extinction of all species (total extinction), regardless of current state. In order to state and prove the theorem, we need the following observation.

Lemma 5.1. *Assume $e_1c_1 > a_1d_1$, and $e_2c_2 > a_2d_2$. Let S_x, S_{y_1}, S_{y_2} be the iso-surfaces defined by $X(x, y_1, y_2) = 0, Y_1(x, y_1, y_2) = 0, Y_2(x, y_1, y_2) = 0$, respectively. If $((S_x \cap S_{y_1}) \cup (S_x \cap S_{y_2})) \cap R_+^3 = (0, 0, 0)$, then all positive solutions of model (2.1) tend to the origin.*

Proof. The condition of $((S_x \cap S_{y_1}) \cup (S_x \cap S_{y_2})) \cap R_+^3 = (0, 0, 0)$ implies that in R_+^3 , S_x does not intersect with S_{y_1} or S_{y_2} except at the origin. It is easy to see that S_{y_1} is the plane defined by $d_1^{-1}(e_1c_1 - a_1d_1)x = y_1 + y_2$ and S_{y_2} is the plane defined by $d_2^{-1}(e_2c_2 - a_2d_2)x = y_1 + y_2$. Observe that S_x intersect the x -axis at $(0, 0, 0)$ and $(K, 0, 0)$. If we view the x -axis as a vertical axis and y_1 - and y_2 -axes as ground ones, then the condition of $((S_x \cap S_{y_1}) \cup (S_x \cap S_{y_2})) \cap R_+^3 = (0, 0, 0)$ implies that S_x sits above both S_{y_1} and S_{y_2} . Hence, if $(x_1, y_1, y_2) \in S_{y_1}, (x_2, y_1, y_2) \in S_{y_2}, (x_3, y_1, y_2) \in S_x$, then $x_3 > \max\{x_1, x_2\}$. Without loss of generality, we may assume that

$$d_1^{-1}(e_1c_1 - a_1d_1) > d_2^{-1}(e_2c_2 - a_2d_2).$$

We see that if $(x_1, y_1, y_2) \in S_{y_1}, (x_2, y_1, y_2) \in S_{y_2}$ then we have $x_1 < x_2$. These together imply that if $(x_1, y_1, y_2) \in S_{y_1}, (x_2, y_1, y_2) \in S_{y_2}, (x_3, y_1, y_2) \in S_x$, then $x_3 > x_2 > x_1$. If we divide the interior of R_+^3 into four separate regions:

$$R_1 = \{(x, y_1, y_2) : x > 0, y_1 > 0, y_2 > 0, x' > 0, y_1' > 0, y_2' > 0\}$$

$$R_2 = \{(x, y_1, y_2) : x > 0, y_1 > 0, y_2 > 0, x' \leq 0, y_1' > 0, y_2' > 0\}$$

$$R_3 = \{(x, y_1, y_2) : x > 0, y_1 > 0, y_2 > 0, x' \leq 0, y_1' > 0, y_2' \leq 0\}$$

$$R_4 = \{(x, y_1, y_2) : x > 0, y_1 > 0, y_2 > 0, x' \leq 0, y_1' \leq 0, y_2' \leq 0\}.$$

A simple flow analysis shows that solutions starting in R_1 enters R_2 in finite time, and then in finite time it enters R_3 , and then in finite time enters R_4 . The process of boundary crossing resembles an one way traffic and the sequence is always $R_1 \rightarrow R_2 \rightarrow R_3 \rightarrow R_4$. Once enters R_4 , it stays there. The monotonicity of all the components of the solution and the fact that R_4 contains no steady state ensures that the solution tends to the origin.

If $d_1^{-1}(e_1c_1 - a_1d_1) = d_2^{-1}(e_2c_2 - a_2d_2)$, then $S_{y_1} = S_{y_2}$, in which case, we see that our proof above can be adapted to deal with it. □

We are now ready to give explicit conditions for model (2.1) to exhibit total extinction as the result of the global stability of the origin.

Theorem 5.2. *Assume that $\min\{c_1, c_2\} > r$, and*

$$\max\left\{\frac{d_1}{e_1c_1 - a_1d_1}, \frac{d_2}{e_2c_2 - a_2d_2}\right\} \leq \min\left\{\frac{c_1 - r}{ra_1}, \frac{c_2 - r}{ra_2}\right\}. \tag{5.3}$$

Then the origin is globally attractive for model (2.1).

Proof. We shall show that if $(x_1, y_1, y_2) \in S_{y_1}, (x_2, y_1, y_2) \in S_{y_2}, (x_3, y_1, y_2) \in S_x$, then $\max\{x_1, x_2\} < x_3$. Observe that if $S_{y_1} \neq S_{y_2}$, then this implies that $((S_x \cap S_{y_1}) \cup (S_x \cap S_{y_2})) \cap R_+^3 = (0, 0, 0)$. If $S_{y_1} = S_{y_2}$, then it is easy to see that the conclusion of Lemma 5.1 remains true. Once this is established, the theorem follows from Lemma 2.1. To show this, we examine the intersection curves of S_x, S_{y_1}, S_{y_2} with the plane $y_1 = lz, y_2 = hz, z \geq 0$, where l, h are positive constants. For convenience, we denote them by L_x, L_{y_1}, L_{y_2} respectively. We have

$$L_x = \{(x, y_1, y_2) : y_1 = lz, y_2 = hz, r - rx - \frac{c_1 lz}{a_1 x + (l + h)z} - \frac{c_2 hz}{a_2 x + (l + h)z} = 0\},$$

$$L_{y_1} = \{(x, y_1, y_2) : y_1 = lz, y_2 = hz, x = \frac{d_1(l + h)z}{e_1 c_1 - a_1 d_1}\},$$

$$L_{y_2} = \{(x, y_1, y_2) : y_1 = lz, y_2 = hz, x = \frac{d_2(l + h)z}{e_2 c_2 - a_2 d_2}\}.$$

We note if $(k_x z, lz, hz) \in L_x, k_x \geq 0$, then

$$r - rk_x z - \frac{c_1 l}{a_1 k_x + (l + h)} - \frac{c_2 h}{a_2 k_x + (l + h)} = 0. \tag{5.4}$$

For each $z > 0$, we may have one or two values of k that satisfies the above equation. For $z > 0$, if k exist, its value must be larger than the value of k^* that satisfies

$$g(k^*) = r - \frac{c_1 l}{a_1 k^* + (l + h)} - \frac{c_2 h}{a_2 k^* + (l + h)} = 0. \tag{5.5}$$

Let

$$k_1 = \frac{c_1 - r}{ra_1}(l + h) \quad k_2 = \frac{c_2 - r}{ra_2}(l + h) \quad k_m = \min\{k_1, k_2\}.$$

It is easy to see that for all $l \geq 0, h \geq 0$,

$$g(k_m) \leq r - \frac{c_1 l}{a_1 k_1 + (l + h)} - \frac{c_2 h}{a_2 k_2 + (l + h)} = 0.$$

Hence,

$$k^* \geq k_m = \min\{\frac{c_1 - r}{ra_1}(l + h), \frac{c_2 - r}{ra_2}(l + h)\}.$$

On the other hand, it is easy to see that if $(k_{y_1} z, lz, hz) \in L_{y_1}, k_{y_1} \geq 0$, then $k_{y_1} = \frac{d_1}{e_1 c_1 - a_1 d_1}(l + h)$, and if $(k_z, lz, hz) \in L_{y_2}, k_{y_2} \geq 0$, then $k_{y_2} = \frac{d_2}{e_2 c_2 - a_2 d_2}(l + h)$. Hence we have shown that if $(x_1, y_1, y_2) \in S_{y_1}, (x_2, y_1, y_2) \in S_{y_2}, (x_3, y_1, y_2) \in S_x$, then $\max\{x_1, x_2\} < x_3$. This completes the proof. \square

One can also imagine that the addition of an identical or similar strength competitor with enough initial population can rise the total predator/prey ratio to the extinction region that can also lead to total extinction of the system.

6. Coexistence

It is easy to observe that system (2.1) does not admit an isolated positive steady state. So, coexistence in the form of asymptotically stable positive steady state is impossible. System (2.1) admits degenerate positive steady states (steady state that has zero as one of its eigenvalue) only when

$$\frac{e_1 c_1}{d_1} - a_1 = \frac{e_2 c_2}{d_2} - a_2. \tag{6.1}$$

One can easily see that degenerate positive steady states are positive solutions of

$$r(1 - x) = \frac{c_1 x y_1}{a_1 x + y_1 + y_2} + \frac{c_2 x y_2}{a_2 x + y_1 + y_2}$$

$$d_1 = \frac{e_1 c_1 x}{a_1 x + y_1 + y_2}.$$

Numerical simulations show (e.g., Figure 3) that under (6.1), positive solutions all quickly tend to one of these degenerate positive steady states that dependent on initial conditions.

The main objective in this section is to show both analytically and numerically that for some range of parameters, all three species can coexist in the form of oscillatory solutions. The method is the now standard approach (e.g., Smith and

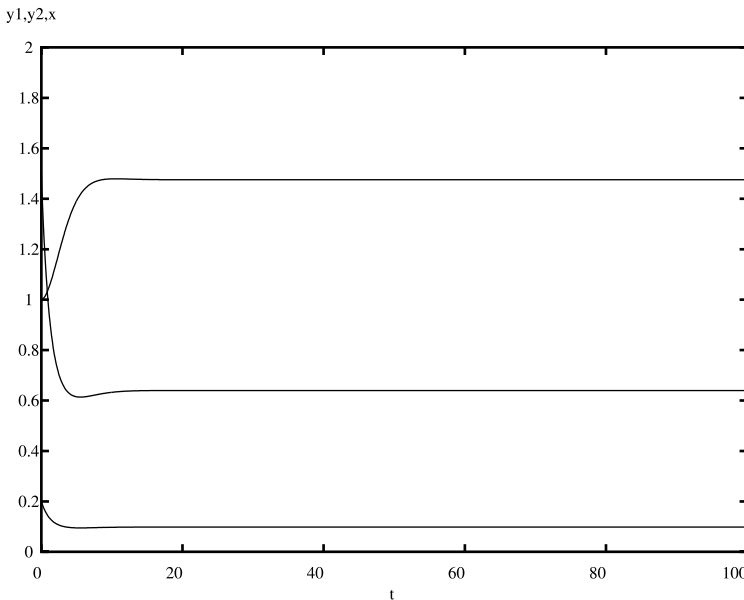


Fig. 3. This figure shows the solution of (2.1) when $r = 1, a_1 = a_2 = d_1 = d_2 = 1, c_1 = 0.700, c_2 = 0.800, e_1 = 2.143, e_2 = 2.250, x(0) = 1, y_1(0) = 0.200, y_2(0) = 1.500$. The solution tends to a degenerate steady state.

Waltman (1995), p65) of finding conditions that can lift a nontrivial positive periodic solution on the boundary, say $x - y_1$ plane (assume it exists) to the interior of the three dimensional positive cone. To facilitate this presentation, we first would like to transform the system (2.1). Let

$$m_1 = e_1c_1, \quad m_2 = e_2c_2, \quad u = x/(y_1 + y_2).$$

Then (2.1) can be transformed to

$$\begin{cases} u' = -ru^2(y_1 + y_2) + \frac{y_1}{y_1 + y_2}g_1(u) + \frac{y_2}{y_1 + y_2}g_2(u) \\ y_1' = y_1(-d_1 + \frac{m_1u}{a_1u + 1}) \\ y_2' = y_2(-d_2 + \frac{m_2u}{a_2u + 1}) \end{cases} \tag{6.2}$$

where

$$g_i(u) = \frac{u}{a_iu + 1}(A_iu + B_i), \quad A_i = ra_i - m_i + d_ia_i, \quad B_i = r - c_i + d_i \quad i = 1, 2. \tag{6.3}$$

In the rest of this section, we assume that (3.1) holds and $a_2 < a_1$. Let

$$\lambda_i = d_i/(m_i - d_ia_i), \quad i = 1, 2.$$

Recall that Theorem 3.1 shows that if $0 < \lambda_1 < \lambda_2$ and $a_2 \geq a_1$, then $\lim_{t \rightarrow \infty} y_2(t) = 0$. Consider for the moment the boundary system

$$\begin{cases} u' = -ru^2y_1 + g_1(u) \\ y_1' = y_1(-d_1 + \frac{m_1u}{a_1u + 1}) \end{cases} \tag{6.4}$$

Hopf bifurcation Theorem and Theorem 2.9 of Hsu et al. (2000) together imply that if $A_1 > 0, B_1 < 0$ and λ_1 is near and less than θ_1 , where θ_1 is the point where the prey isocline $y_1 = g_1(u)/(ru^2)$ attains its maximum, then there is a unique limit cycle on the boundary ($u - y_1$ plane) $\Gamma^* = \{(u^*(t), y_1^*(t)) : 0 \leq t \leq T_1\}$. In order to obtain the coexistence of species y_1 and y_2 , it is convenient to select $b_2 := m_2/d_2$ as a bifurcation parameter and study the possibility of the bifurcation of limit cycle $\Gamma = \{(u^*(t), y_1^*(t), 0) : 0 \leq t \leq T_1\}$ into the positive octant.

Theorem 6.1. *In system (6.2), let $0 < \lambda_1 < \lambda_2$ and $a_2 < a_1$. Then there exists $b_2^*, a_2 < b_2^* < a_2 - a_1 + m_1/d_1$ such that for $b_2 = m_2/d_2$ sufficiently close to b_2^* , system (6.2) has a periodic orbit inside the positive octant near the $u - y_1$ plane.*

Proof. We observe that the condition $0 < \lambda_1 < \lambda_2$ is equivalent to

$$b_2 = m_2/d_2 < a_2 - a_1 + m_1/d_1.$$

Γ is a stable (unstable) limit cycle if

$$\int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2u^*(t) + 1} dt < 0 \quad (> 0).$$

Notice that

$$\int_0^{T_1} \left(\frac{m_2 u^*(t)}{a_2 u^*(t) + 1} - d_2 \right) dt = (m_2 - d_2 a_2) \int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt.$$

Let

$$\mu(b_2) = \frac{1}{T_1} \int_0^{T_1} \frac{b_2 u^*(t)}{a_2 u^*(t) + 1} dt.$$

Then, Γ is stable (unstable) if $\mu(b_2) < 1$ ($\mu(b_2) > 1$). Clearly, $\mu(b_2)$ is strictly increasing in b_2 and $\mu(a_2) < 1$. In order to show that there exists $b_2^*, a_2 < b_2^* < a_2 - a_1 + m_1/d_1$ such that $\mu(b_2^*) = 1$, it suffices to show that for $b_2 = a_2 - a_1 + m_1/d_1$, $\mu(b_2) > 1$. Equivalently, when $\lambda_1 = \lambda_2 = \lambda$, we have $\int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt > 0$. Since

$$\int_0^{T_1} \frac{u^*(t) - \lambda_1}{a_1 u^*(t) + 1} dt = 0,$$

we have

$$\begin{aligned} \int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt &= \int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt - \eta \int_0^{T_1} \frac{u^*(t) - \lambda_1}{a_1 u^*(t) + 1} dt \\ &= \int_0^{T_1} (u^*(t) - \lambda) \left[\frac{1}{a_2 u^*(t) + 1} - \frac{\eta}{a_1 u^*(t) + 1} \right] dt \\ &= (a_1 - a_2 \eta) \int_0^{T_1} \frac{(u^*(t) - \lambda) \left(u^*(t) - \frac{\eta - 1}{a_1 - a_2 \eta} \right)}{(a_1 u^*(t) + 1)(a_2 u^*(t) + 1)} dt. \end{aligned}$$

Let $\eta = \frac{1 + \lambda a_1}{1 + \lambda a_2}$. Due to the assumption of $a_1 > a_2$, we see that

$$a_1 - a_2 \eta = \frac{a_1 - a_2}{1 + \lambda a_2} > 0.$$

Hence

$$\int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt = \int_0^{T_1} \frac{(a_1 - a_2 \eta)(u^*(t) - \lambda)^2}{(a_1 u^*(t) + 1)(a_2 u^*(t) + 1)} dt > 0.$$

That is, $\mu(b_2) > 1$. This shows that there exists $b_2^*, a_2 < b_2^* < a_2 - a_1 + m_1/d_1$ such that $\mu(b_2^*) = 1$. From Theorem 7.1 of Smith and Waltman (1995)(p65), we see that for b_2 close to b_2^* , system (6.2) has a periodic orbit in the positive octant near the $u - y_1$ plane. □

Figure 4 illustrates the y_1, y_2 components of such a periodic orbit. Here initial values are $u = 4.41, y_1 = 0.06, y_2 = 0.005$ and model parameters are $a_1 = 1, a_2 = 0.85, d_1 = 3.26, d_2 = 2.37, m_1 = 4, m_2 = 2.54, c_1 = 4.78, c_2 = 4.75$. As one changes the initial values, the dynamics can change dramatically. For example, increasing the y_2 initial value can lead to the extinction of both predator species as well as the prey species.

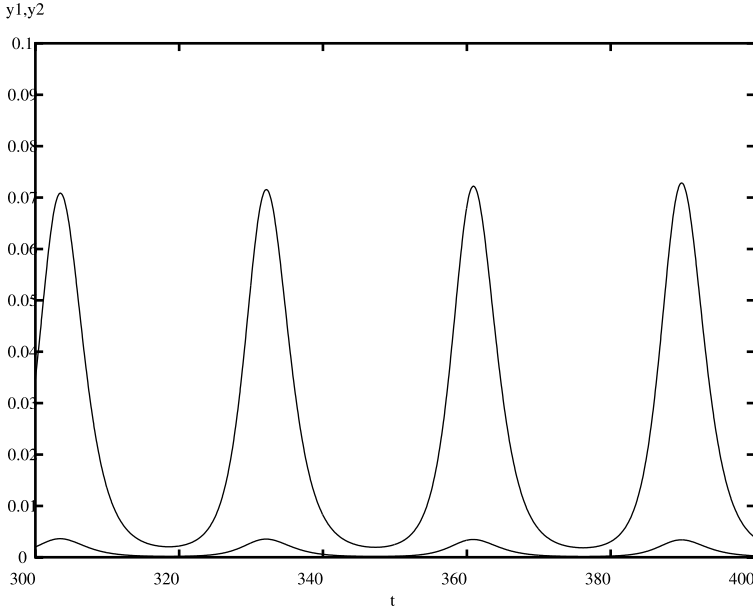


Fig. 4. This figure shows the y_1, y_2 components of a periodic orbit of system (6.2). Here initial values are $u = 4.41, y_1 = 0.06, y_2 = 0.005$ and model parameters are $r = 1, a_1 = 1, a_2 = 0.85, d_1 = 3.26, d_2 = 2.37, m_1 = 4, m_2 = 2.54, c_1 = 4.78, c_2 = 4.75$.

Remark 6.1. If $0 < \lambda_1 < \lambda_2, a_1 < a_2$, then from Theorem 3.1, we see that $\lim_{t \rightarrow \infty} y_2 \rightarrow 0$. Under these conditions, the proof of Theorem 6.1 also shows that

$$\int_0^{T_1} \frac{u^*(t) - \lambda_2}{a_2 u^*(t) + 1} dt = \int_0^{T_1} \frac{(a_1 - a_2 \eta)(u^*(t) - \lambda)^2}{(a_1 u^*(t) + 1)(a_2 u^*(t) + 1)} dt < 0$$

since

$$a_1 - a_2 \eta = \frac{a_1 - a_2}{1 + \lambda a_2} < 0.$$

Hence $\mu(b_2) < 1$ for all

$$b_2 = m_2/d_2 < a_2 - a_1 + m_1/d_1,$$

which is equivalent to say that Γ is stable. This is consistent with Theorem 3.1.

7. Discussion

Our systematical work on system (2.1) reveals that the ratio-dependent model is richer in boundary dynamics (extinction dynamics) compare to the prey-dependent

one

$$\begin{cases} x' = rx(1-x) - \frac{c_1xy_1}{x+a_1} - \frac{c_2xy_2}{x+a_2} \\ y'_1 = y_1(-d_1 + \frac{e_1c_1x}{x+a_1}) \\ y'_2 = y_2(-d_2 + \frac{e_2c_2x}{x+a_2}). \end{cases} \tag{7.1}$$

This prey-dependent model resembles the chemostat model with two competing predator species (Butler et al.(1983), Smith and Waltman(1995)). It can be shown similarly that it produces competitive exclusion and possibly coexistence similar to the ones for (2.1) (Hsu et al.(1978a, b)), but can not generate total extinction and can not exhibit the system saver phenomenon due to the lack of degeneracy at origin. In general, the above model has a limiting dynamics of a two-dimensional predator-prey model reduced from itself.

Mathematically and biologically (Cosner et al.(1999)), both (2.1) and (7.1) can and should be viewed as limiting cases of the more realistic Beddington-DeAngelis one

$$\begin{cases} x' = rx(1-x) - \frac{c_1xy_1}{x+a_1+b_1(y_1+y_2)} - \frac{c_2xy_2}{x+a_2+b_2(y_1+y_2)} \\ y'_1 = y_1(-d_1 + \frac{e_1c_1x}{x+a_1+b_1(y_1+y_2)}) \\ y'_2 = y_2(-d_2 + \frac{e_2c_2x}{x+a_2+b_2(y_1+y_2)}), \end{cases} \tag{7.2}$$

Again, due to the lack of degeneracy at the origin in model (7.2) when $a_1 > 0$ and $a_2 > 0$, we observe that it also will not produce the above mentioned extinction dynamics. Still, we can speculate that such extinction dynamics can be viewed as the possible approximate scenario of model (7.2) when a_1 and a_2 are small and other relevant conditions are met, and can ultimately be brought into reality when stochastic events are taken into account. Due to the competitive exclusion outcome, neither of these models are expected to generate chaotic solutions.

Another striking phenomenon that can often be observed in simulation work of model (2.1) is its highly sensitivity on initial population levels, especially when these levels are relatively low. This is also not shared by either (7.1) or (7.2).

A recent finding of Jost and Arditi(2000) shows that prey-dependent and ratio-dependent model can fit well with the time series generated by each other. Interestingly, the ratio-dependent time series reportedly were always more reliably identified. This together with our analysis of (2.1) in this paper and previous work suggest that ratio-dependent models are more flexible and versatile.

We would like to point out here that our analysis of model (2.1), while covers many aspects, is far from complete. Many questions of the dynamics of this model remain untouched. For example, it is unclear at this moment whether or not a system saver can save both the ailing prey and predator species in an collapsing predator-prey interaction. Most of our results provide sets of sufficient conditions for various dynamical scenarios to occur. It will be interesting both mathematically and biologically to know what kind of necessary conditions for such dynamics

behaviors. For example, assume that we know if scenario A dynamics takes place, then condition set B must be met. Assume further that we can manage to violate condition set B, then we can avoid scenario A dynamics. In some special cases, such necessary conditions are easy to obtain. A more systematic and complete coverage of such necessary conditions is likely to be a nontrivial task. Naturally, these interesting topics should be pursued in the future. It is also easy to see that there is room for the improvement of our various sufficient conditions. In short, we know model (2.1) is capable of generating rich and new dynamics, but its detailed qualitative and general dynamical picture remains to be seen.

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