Analysis of Dynamics in Two-prey, one-predator model: Effect of the Remained carcass

岡山大学環境学研究科 李聖林 (Sungrim Seirin Lee)
Graduate School of Environmental Science,
Okayama University

1 Introduction

The purpose of this paper is to propose the model which describes the effect of remained carcasses and study the persistence and the dynamics. We suppose that the remained carcass of a prey becomes foods of outsider species after predators have consumed the prey. It is well-known that many carnivorous insects such as cricket eat not only vegetable but also the carcass of small animals.

For convenience, henceforth the prey will be called the existent prey and the outsider species such as carnivorous insects, the existent prey. The variables of $h_1(t), h_2(t)$ and p(t) denote the densities of the existent prey, the invader prey and the predator respectively. In this paper, we consider as the following functional response of the existent prey to the benefit of remained carcasses:

$$\Psi(h_1,h_2,p) = \frac{\tau_1 h_2 p}{\tau_2 h_1 + \tau_3 h_2},$$

where τ_1, τ_2 and τ_3 are positive constants. we suppose that existent preys have two negative effects by the intra-species competition of themselves and the obstruction of invader preys, to have remained carcasses. We assume that the two negative effects are proportional to the density of the existent prey and the density of the invader prey respectively, and for simplifying the model, the real amount of remained carcasses which the existent prey has is proportional to the total amount of remained carcasses divided by the negative effects.

Hence, Incorporating the functional response Ψ in the existent prey, the model takes the form:

$$\frac{d}{dt}h_{1} = \varepsilon_{1} \left(1 - \frac{h_{1}}{k_{1}}\right) h_{1} - a_{1}h_{1}p + \frac{\tau_{1}h_{2}p}{\tau_{2}h_{1} + \tau_{3}h_{2}} h_{1}$$

$$\frac{d}{dt}h_{2} = \varepsilon_{2} \left(1 - \frac{h_{2}}{k_{2}}\right) h_{2} - a_{2}h_{2}p$$

$$\frac{d}{dt}p = -\delta p + b_{1}h_{1}p + b_{2}h_{2}p$$
(1)

where

 ε_i growth rate of preys in the absence of predator

 k_i carrying capacity of preys

 a_i consumption rate of preys by predator

 b_i rate of increase in the number of predators from ingesting prey

 δ death rate of predator,

and ε_i , k_i , a_i , b_i and δ are positive constants. Now to avoid mathematical complexity, we nondimensionlize the system(1) without loss of generality:

$$\frac{d}{dt}y_{1} = (1 - y_{1})y_{1} - \alpha_{1}y_{1}p + \frac{\omega y_{2}p}{ky_{1} + y_{2}}y_{1}$$

$$\frac{d}{dt}y_{2} = \varepsilon(1 - y_{2})y_{2} - \alpha_{2}y_{2}p$$

$$\frac{d}{dt}p = -\gamma p + \beta_{1}y_{1}p + \beta_{2}y_{2}p$$
(2)

where

$$\alpha_i = \frac{a_i}{\varepsilon_1}, \quad \omega = \frac{\tau_1}{\varepsilon_1}, \quad k = \tau_2 \frac{k_1}{k_2}, \quad \varepsilon = \frac{\varepsilon_2}{\varepsilon_1}, \quad \gamma = \frac{\delta}{\varepsilon_1} \quad \text{and} \quad \beta_i = \frac{b_i k_i}{\varepsilon_1}.$$
 (3)

In this paper, we suppose that

(I) The existent prey and the predator have already approached to stable coexistence density before the invader prey invade.

(II) The gain of the existent prey given by the predator is less than loss when the existent prey and the invader prey approach their carrying capacities respectively.

These assumptions lead to the following mathematical assumptions and initial condition:

$$1 > \frac{\gamma}{\beta_1},\tag{4}$$

$$\frac{\omega}{k+1} < \alpha_1 \tag{5}$$

and

$$(y_1(0), y_2(0), p(0)) = \left(\frac{\gamma}{\beta_1}, n_0, \frac{1}{\alpha_1}(1 - \frac{\gamma}{\beta_1})\right). \tag{6}$$

2 Analysis and Dynamics of the model

2.1 Steady states and Linear stability

In this section, we analyse stability of equilibria of system(2). On the boundary of $\mathbf{R}_{+}^{3} = \{(y_1, y_2, p) : y_1 \geq 0, y_2 \geq 0, p \geq 0\}$, we have equilibria $E_0 = (0, 0, 0), E_1 = (0, 0, 0)$

 $(1,0,0), E_2 = (0,1,0), E_3 = (1,1,0)$

$$E_4=(ar{y}_1,0,ar{p})=\left(rac{\gamma}{eta_1},0,rac{1}{lpha_1}(1-rac{\gamma}{eta_1})
ight)$$

since $\beta_1 > \gamma$ from condition(4). The equilibrium

$$E_5 = (0, \tilde{y}_2, \tilde{p}) = \left(0, \frac{\gamma}{\beta_2}, \frac{\varepsilon}{\alpha_2}(1 - \frac{\gamma}{\beta_2})\right)$$

exists if $\beta_2 > \gamma$. We summarize the results of linear stability analysis for these equilibria.

1.
$$E_0, E_1, E_2$$
 and E_3 are saddle points and so are unstable. (7)

2. E_4 is locally asymtotically stable if $\varepsilon - \frac{\alpha_2}{\alpha_1}(1 - \frac{\gamma}{\beta_1}) < 0$,

but is unstable if
$$\varepsilon - \frac{\alpha_2}{\alpha_1} \left(1 - \frac{\gamma}{\beta_1} \right) > 0.$$
 (8)

3. E_5 is locally asymtotically stable if $1 + \frac{\varepsilon}{\alpha_2}(\omega - \alpha_1)(1 - \frac{\gamma}{\beta_2}) < 0$,

but is unstable if
$$1 + \frac{\varepsilon}{\alpha_2}(\omega - \alpha_1) \left(1 - \frac{\gamma}{\beta_2}\right) > 0.$$
 (9)

We note here that the equilibrium $E_4 = (\bar{y}_1, 0, \bar{p})$ is initial condition in our model. Thus if it is unstable, invader preys can succeed in invading even if the density of the invader prey is very small.

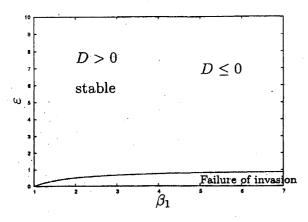
We write the equilibrium of which all the coordinates are positive as $E^* = (y_1^*, y_2^*, p^*)$, and then say that E^* is an interior equilibrium. Now, we state the existence and uniqueness of the interior equilibrium E^* of system (2) under the conditions that the equilibria E_4 and E_5 are unstable.

Proposition 1 There exists the interior equilibrium $E^* = (y_1^*, y_2^*, p^*)$ of system (2) uniquely if and only if the condition (8) and (9) are satisfied.

We obtain the existence of the equilibrum point E^* , but applications of Routh-Hurwitz criterion give rise to complex set of mathematical conditions for stability drawn from these. In fact, when the linearization matrix on E^* leads to the eigenvalue equation $\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0$, Routh-Hurwitz criterion gives that all of eigenvalues have negative real part if and only if

$$A_1 > 0$$
, $A_3 > 0$ and $D = A_1 A_2 - A_3 > 0$.

We have $A_1 > 0$ and $A_3 > 0$ but the sign of D depends on parameters. By numerical simulations, we find out Hope bifurcation for some parameter values. For instance, Figure 1 show that the stable region of the interior equilibrium E^* for parameters ε and β_1 . We carry out numerical simulation for parameters ε and β_1 with the fixed other parameters, for example, $k = 0.2, \alpha_1 = \alpha_2 = 2, \beta_2 = 5, \gamma = 1$ and



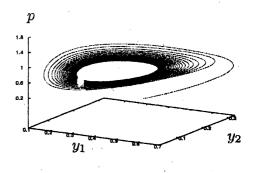


Figure 1: Stable region

Figure 2: Limit cycle with $\varepsilon = 3$

 $\omega=2.35$, which parameter values satisfy the conditions (8), (9) and (5). The invasion condition(8) is satisfied in the region under the line of Figure 1. For proper parameter values in the region satisfying $D \leq 0$, the equilibrium E^* may be unstable. In fact, Figure 2 show that a limit cycle appears by choosing $\varepsilon=3$ and $\beta_1=3$. Moreover, Figure 1 show that the limit cycle disappears and a stable equilibrium appears again if we take ε large more and more.

2.2 Persistence

In this section, we prove strong persistence of the system (2). We use the definition of strong persistence, namely, a population h(t) is said to persist if h(0) > 0 and $\liminf_{t\to\infty} h(t) > 0$. A system is said to persist if each component population persists. To prove the persistence, we use Theorem (2.1) of Freedman and Waltman[1], which has proved by using dynamical system theory. First of all, to obtain the existence of the dynamical system for the system (2), we have the following two propositions.

Proposition 2 The solution $y_1(t), y_2(t), p(t)$ of system (2) is bounded for all $t \ge 0$ and arbitrary initial values if the assumption $(5), \frac{\omega}{k+1} < \alpha_1$, is satisfied.

Proposition 3 System (2) with nonnegative initial values has an unique local solution.

From Proposition 2 and Proposition 3, we obtain the following Lemma.

Lemma 1 System (2) with nonnegative initial values has a global solution uniquely if condition (5) is satisfied.

Then we obtain the strong persistence theorem for system (2).

Theorem 1 (Strong Persistence) System (2) persists strongly if the following assumptions (5), (8) and (9):

$$\frac{\omega}{k+1} < \alpha_1, \quad \varepsilon - \frac{\alpha_2}{\alpha_1} (1 - \frac{\gamma}{\beta_1}) > 0 \quad \text{ and } \quad 1 + \frac{\varepsilon}{\alpha_2} (\omega - \alpha_1) (1 - \frac{\gamma}{\beta_2}) > 0, (10)$$

are satisfied.

2.3 Numerical simulation results I

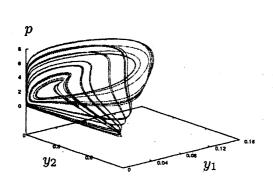
In this section, we study the dynamics of system (2) more detail by using numerical simulations. We assume the conditions (4), (5) and $\beta_2 > \gamma$, then the conditions (8) and (9) are rewritten for the parameter ε as the following:

$$\frac{\alpha_2}{\alpha_1} \left(1 - \frac{\gamma}{\beta_1} \right) < \varepsilon < \frac{\alpha_2}{(\alpha_1 - \omega)(1 - \frac{\gamma}{\beta_2})} \quad \text{for} \quad \alpha_1 > \omega, \tag{11}$$

$$\varepsilon > \frac{\alpha_2}{\alpha_1} \left(1 - \frac{\gamma}{\beta_1} \right) \quad \text{for} \quad \frac{\omega}{k+1} < \alpha_1 \le \omega.$$
 (12)

On these cases, the invader prey succeed in invading and the extinction point of the existent prey, E_5 , is unstable. Moreover, these conditions guarantee the strong persistence of three species.

We choose parameter values satisfying persistence condition (10), and carry out numerical simulations. Then we find out that populations of the system (2) have a chaotic attractor. An example of the chaotic attractor is shown in Figure 3. We



Populations 2 25 20 25 40 45 25

Figure 3: Chaos in the $y_1 - y_2 - p$ phase.

Figure 4: Population fluctuations of the existent prey(red), the invader prey(green) and the predator(blue)

have carried out the numerical simulation with parameters $\beta_1 = 21, \varepsilon = 3$,

$$k = 0.2$$
, $\alpha_1 = \alpha_2 = 2$, $\beta_2 = 5$, $\gamma = 1$, and $\omega = 2.35$. (13)

Figure 4 show population fluctuations of three species when the system (2) has the chaotic attractor (Fig.3). We want to notice the fluctuations' patterns in Figure 4. Without the remained carcass effect, the invasion of invader preys make predators increasing, and then existent preys must decrease. However, Figure 4 show that the existent prey increases and never turn into decrease during the invader prey increase even if the predator increase sharply. Moreover, the decrease of the existent prey starts after the decrease of the invader prey. It shows that the invader prey is a cooperator to the existent prey. We can also find out that the existent prey increases more sharply where the predator increases sharply and even if the invader prey turn into decreasing. Even if the invader preys start to decrease, total amount of the

remained carcass does not change very if the predators increase sufficiently. Thus the existent prey can have enough amount of the remained carcasses to increase its density. The predator and the existent prey have a symbiosis interaction.

3 Conclusions

In this paper, we have studied population dynamics of the two-prey, one-predator model which describes the effect of remained carcasses. The simple two-prey, one-predator Lotka-Volterra model has a globally asymptotic stable interior equilibrium. Thus, the dynamics of the model always goes to stable coexistent equilibrium point. However, we have shown that the remained carcass effect gives very complex dynamics under the strong persistent condition (10). Until now, many prey-predator population models have been studied but usually, they did not consider the existence of the remained carcass. It will be very important to consider the remained carcass effect in the interactions of species, especially in multi-species models.

References

[1] Freedman H.I, Waltman P. Persistence in models of three interacting predatorprey population. Math Biosci 68 (1984) 213-231.