The Effect of the Remains of Carcass in Two-prey, one-predator model with Diffusion

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1 Introduction

In nature, there are many various and complex interactions between creatures on several steps of trophic level. Many studies related with such a population interaction have done and shown coexistence and various dynamics of populations. As one of the related studies, continuous time models for food chain, exploitative competition, apparent competition and intraguild predation have been researched extensively in literature (e.g.[1], [3] and so on). As an example of the interaction which is not described above, we find out that an omnivorous cricket eats vegetables as well as the carcass of some small animals. Usually, no all of predators eat a whole prey and thus some parts of the carcass of the prey remain. Then the remains of carcass can be foods for the other animals.

For convenience, henceforth the omnivorous prey will be called the existent prey and the small animal, the invader prey. Then, the following system gives the simplest model which is concerned with the effect of the remains of carcass in two-prey, one-predator model([2]).

$$\frac{d}{dt}h_1 = \varepsilon_1\left(1 - \frac{h_1}{k_1}\right)h_1 - a_1h_1p + \tau_1h_2ph_1$$

$$\frac{d}{dt}h_2 = \varepsilon_2\left(1 - \frac{h_2}{k_2}\right)h_2 - a_2h_2p \qquad (1)$$

$$\frac{d}{dt}p = -\delta p + b_1h_1p + b_2h_2p$$

where h_1, h_2 and p denote the densities of the existent prey, the invader prey and the predator respectively. In the model (1) the amount of the remains of carcass is simply proportional to the rate that the predator meet the invader prey. To intend the effect of the carcass, we suppose that the existent prey and the invader prey do not have inter-specific competition and the other direct interactions.

Now, in this paper we consider a diffusion model which is concerned with the negative effect by intra-specific competition of existent preys and obstruction of

invader preys. The functional response of the remains of carcass with negative effect is given as the following:

$$\Psi(h_1, h_2, p) = \frac{\tau_1 h_2 p}{\tau_2 h_1 + \tau_3 h_2 + 1}.$$

In this paper, we notice the case that τ_1, τ_2 and τ_3 are sufficiently large. By simplifying the functional response $\Psi(h_1, h_2, p)$ mathematically with $\tau_1/\tau_3 = \mu_1$ and $\tau_2/\tau_3 = \mu_2$ as $\tau_3 \to \infty$, we obtain the following model:

$$\frac{\partial}{\partial t} h_1 = d_1 \frac{\partial^2}{\partial x^2} h_1 + \varepsilon_1 \left(1 - \frac{h_1}{k_1}\right) h_1 - a_1 h_1 p + \frac{\mu_1 h_2 p}{\mu_2 h_1 + h_2} h_1$$

$$\frac{\partial}{\partial t} h_2 = d_2 \frac{\partial^2}{\partial x^2} h_2 + \varepsilon_2 \left(1 - \frac{h_2}{k_2}\right) h_2 - a_2 h_2 p \qquad (2)$$

$$\frac{\partial}{\partial t} p = d_3 \frac{\partial^2}{\partial x^2} p - \delta p + b_1 h_1 p + b_2 h_2 p.$$

Then we have the following nondimensionlized system without loss of generality.

$$\frac{\partial}{\partial t} h_1 = d_1 \frac{\partial^2}{\partial x^2} h_1 + (1 - h_1) h_1 - \alpha_1 h_1 p + \frac{\omega h_2 p}{k h_1 + h_2} h_1$$

$$\frac{\partial}{\partial t} h_2 = d_2 \frac{\partial^2}{\partial x^2} h_2 + \varepsilon(1 - h_2) h_2 - \alpha_2 h_2 p \qquad (3)$$

$$\frac{\partial}{\partial t} p = d_3 \frac{\partial^2}{\partial x^2} p - \gamma p + \beta_1 h_1 p + \beta_2 h_2 p.$$

where

$$\alpha_i = \frac{a_i}{\varepsilon_1}, \quad \omega = \frac{\mu_1}{\varepsilon_1}, \quad k = \mu_2 \frac{k_1}{k_2}, \quad \varepsilon = \frac{\varepsilon_2}{\varepsilon_1}, \quad \gamma = \frac{\delta}{\varepsilon_1} \quad \text{and} \quad \beta_i = \frac{b_i k_i}{\varepsilon_1}. \qquad (4)$$

We suppose that the environment is uniform, and the existent prey and the predator have already attained the coexistence state in the space uniformly when some propagules of the invader prey (say n_0 individuals) invade in the origin at $t = 0$. This gives the initial condition as the following:

$$y_1(x, 0) = \frac{\gamma}{\beta_1}, \quad y_2(x, 0) = n_0 \hat{\delta}(x), \quad p(x, 0) = \frac{1}{\alpha_1} \left(1 - \frac{\gamma}{\beta_1}\right) \qquad (5)$$

where $\hat{\delta}(x)$ is delta function.

In this paper, we show that there exist a traveling wave by numerical simulation and propose the speed of it by mathematical analysis including numerical simulations. We obtain the speed condition which depends only on the diffusion coefficient of the invader. We also find out a chaotic phenomenon.

2 Numerical simulation results

In the system (3), we have a stationary solution

$$E^0 = (\bar{h}_1(x), 0, \bar{p}(x)) = \left(\frac{\gamma}{\beta_1}, 0, \frac{1}{\alpha_1}(1 - \frac{\gamma}{\beta_1})\right)$$

if $\beta_1 > \gamma$ is satisfied. Furthermore, the stationary solution E^0 becomes unstable when

$$\varepsilon - \frac{\alpha_2}{\alpha_1}(1 - \frac{\gamma}{\beta_1}) > 0.$$

We also have the following result([2]).

Proposition 1 There exists a positive stationary solution $E^* = (h_1^*(x), h_2^*(x), p^*(x))$ uniquely if the following conditions are satisfied:

$$\varepsilon - \frac{\alpha_2}{\alpha_1}(1 - \frac{\gamma}{\beta_1}) > 0, \qquad 1 + \frac{\varepsilon}{\alpha_2}(\omega - \alpha_1)(1 - \frac{\gamma}{\beta_2}) > 0. \qquad (6)$$

Now we carry out numerical simulations with parameter values satisfying the conditions (6). Then we find out a traveling wave with $d_1 = d_2 = d_3 = 1$ and $\varepsilon = 1$, which connects E^0 and E^* at $x \to \infty$ and $x \to -\infty$ respectively (Fig.1). When we take $\varepsilon = 3$, we see chaotic dynamics for some fixed x(Fig.2).
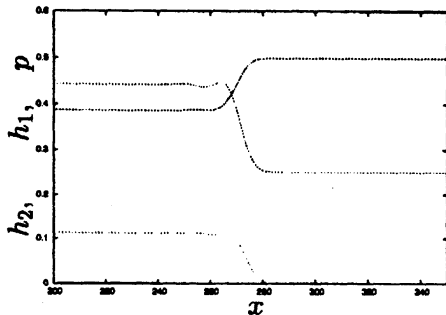

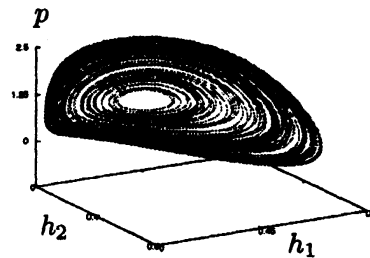Figure 1: Traveling wave with $\varepsilon = 1$ Figure 2: Chaos with $\varepsilon = 3$ for time

We have carried out these simulations with all the same diffusion values, but we show that the traveling wave speed depends on only d_2 through mathematical approach and numerical simulation in the following section.

3   Speed of traveling wave

From the numerical simulation results we have found a traveling wave solution which connects the stationary solution $E^0 = (\bar{h}_1(x), 0, \bar{p}(x))$ and $E^* = (h_1^*(x), h_2^*(x), p^*(x))$. Now we propose the speed of traveling wave only depends on diffusion coefficient d_2 of the invader prey.

We seek traveling wave solutions of system(3) in the form

$$U(z) = (h_1(x,t), h_2(x,t), p(x,t)) = (U_1(z), U_2(z), U_3(z)) \qquad (7)$$

where $z = x - ct$ and $c > 0$. Then these solutions should satisfy

$$U(-\infty) = (h_1^*, h_2^*, p^*) \quad \text{and} \quad U(\infty) = (\bar{h}_1, 0, \bar{p}). \qquad (8)$$

With setting $V_1(z) = U_1'(z), V_2(z) = U_2'(z)$ and $V_3(z) = U_3'(z)$, substituting (7) into system (2) gives the following dynamical system:

$$U_1' = V_1$$
$$U_2' = V_2$$
$$U_3' = V_3$$
$$V_1' = -\frac{1}{d_1}\left\{cV_1 + (1 - U_1)U_1 - \alpha_1 U_1 U_3 + \frac{\omega U_2 U_3}{kU_1 + U_2}U_1\right\}$$
$$V_2' = -\frac{1}{d_2}\{cV_2 + \varepsilon(1 - U_2)U_2 - \alpha_2 U_2 U_3\}$$
$$V_3' = -\frac{1}{d_3}\{cV_3 - \gamma U_3 + \beta_1 U_1 U_3 + \beta_2 U_2 U_3\}.$$

(9)

Thus from the conditions (8), we also have the following conditions:

$$\xi^* = (U_1(-\infty), U_2(-\infty), U_3(-\infty), V_1(-\infty), V_2(-\infty), V_3(-\infty))$$
$$= (h_1^*, h_2^*, p^*, 0, 0, 0),$$
$$\bar{\xi} = (U_1(\infty), U_2(\infty), U_3(\infty), V_1(\infty), V_2(\infty), V_3(\infty))$$
$$= (\bar{h}_1, 0, \bar{p}, 0, 0, 0).$$

We can check easily that $\xi^* = (h_1^*, h_2^*, p^*, 0, 0, 0)$ and $\bar{\xi} = (\bar{h}_1, 0, \bar{p}, 0, 0, 0)$ are equilibria of the dynamical system (9).

Now, we find the solution of the dynamical system (9) which connects the two equilibrium points ξ^* and $\bar{\xi}$ and also satisfies $U_1(z) > 0, U_2(z) > 0$ and $U_3(z) > 0$. We notice the positiveness of the solution U_2 because $U_2(z) \to 0$ as $z \to \infty$. That is, if the solution U_2 oscillates, it must have negative values around origin. Then U_2 cannot lead to traveling wave solution since the traveling wave should be a positive solution of the system (3). To show that $U_2(z)$ does not oscillate around the origin, we investigate the behaviors of U_2 around the origin by linearization of the system(9) about $\bar{\xi}$.

Let $J(\bar{\xi})$ denote Jacobian matrix of the dynamical system(9) at $\bar{\xi}$. Then the eigenvalues λ of Jacobian $J(\bar{\xi})$ are given by the solutions of the following eigenvalue equation:

$$\det|\lambda I - J(\bar{\xi})| = \left\{\lambda^2 + \frac{c}{d_2}\lambda + \frac{1}{d_2}(\varepsilon - \alpha_2\bar{p})\right\}$$
$$\left\{\lambda^4 + c\left(\frac{d_1 + d_3}{d_1 d_3}\right)\lambda^3 + \left(\frac{c^2}{d_1 d_3} - \frac{\bar{h}_1}{d_1}\right)\lambda^2 - \frac{c\bar{h}_1}{d_1 d_3} + \alpha_1\beta_1\frac{\bar{h}_1\bar{p}}{d_1 d_3}\right\} = 0.$$

where I is the identity matrix. Set the first term and the second term of the eigenvalue eqation as $\phi_1(\lambda)$ and $\phi_2(\lambda)$ respectively:

$$\phi_1(\lambda) = \lambda^2 + \frac{c}{d_2}\lambda + \frac{1}{d_2}(\varepsilon - \alpha_2\bar{p})$$
$$\phi_2(\lambda) = \lambda^4 + c\left(\frac{d_1 + d_3}{d_1 d_3}\right)\lambda^3 + \left(\frac{c^2}{d_1 d_3} - \frac{\bar{h}_1}{d_1}\right)\lambda^2 - \frac{c\bar{h}_1}{d_1 d_3} + \alpha_1\beta_1\frac{\bar{h}_1\bar{p}}{d_1 d_3}$$

Then for the eigenvalue λ satisfying $\phi_1(\lambda) = 0$ or $\phi_2(\lambda) = 0$, we can obtain the eigenvector X from the following equation:

$$(\lambda I - J(\bar{\xi}))X = 0, \tag{10}$$

where $X^t = (U_1, U_2, U_3, V_1, V_2, V_3)$.

We first consider the eigenvalues included in $\{\lambda : \phi_1(\lambda) \neq 0, \phi_2(\lambda) = 0\}$. Then from the equation (10) we obtain the following system about U_2 and V_2:

$$\begin{cases} \dfrac{\varepsilon - \alpha_2 \bar{p}}{d_2} U_2 + (\lambda + \dfrac{c}{d_2})V_2 = 0, \\ \lambda U_2 - V_2 = 0. \end{cases}$$

Solving the system give the following equation:

$$\left\{ \lambda^2 + \frac{c}{d_2}\lambda + \frac{1}{d_2}(\varepsilon - \alpha_2 \bar{p}) \right\} U_2 = 0,$$

and thus we have

$$U_2 = 0,$$

since $\phi_1(\lambda) \neq 0$. Therefore, we conclude that U_2 does not oscillate around the origin in the case of $\lambda \in \{\lambda : \phi_1(\lambda) \neq 0, \phi_2(\lambda) = 0\}$.

Now we consider the remained case of the eigenvalues in $\{\lambda : \phi_1(\lambda) = 0\}$. Then similarly from eigenvector equation (10) we have

$$\begin{cases} -\lambda(\lambda + \dfrac{c}{d_2}U_2) + (\lambda + \dfrac{c}{d_2})V_2 = 0, \\ \lambda U_2 - V_2 = 0. \end{cases}$$

Solving the system gives

$$\lambda U_2 = V_2,$$

and thus we obtain $U_2(z)$ from $V_2 = U_2'$:

$$U_2(z) = e^{\lambda z}\zeta,$$

where ζ is a constant. If λ is not real number but complex number, U_2 must be oscillate around the origin. It cannot lead to traveling wave solution. Hence,

$$\phi_1(\lambda) = \lambda^2 + \frac{c}{d_2}\lambda + \frac{1}{d_2}(\varepsilon - \alpha_2 \bar{p}) = 0$$

should have only real solutions. For the existence of only real solutions, the following inequality is obtained:

$$\left(\frac{c}{d_2}\right)^2 - 4\frac{\varepsilon - \alpha_2 \bar{p}}{d_2} \geq 0.$$

At last we lead the condition that the speed of the traveling wave should satisfy:

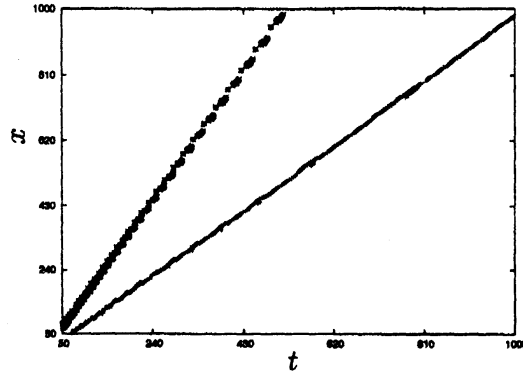$$c \geq 2\sqrt{d_2(\varepsilon - \alpha_2 \bar{p})}, \tag{11}$$

Figure 3: Slopes of lines give the traveling wave speed with $d_2 = 0.5$(red) and $d_2 = 2$(blue). In the case of $d_2 = 0.5$ we have the speed $c = 1$.

where $\bar{p} = \frac{1}{\alpha_1}(1 - \frac{\gamma}{\beta_1})$. Note that we obtain this condition for arbitrary d_1, d_2, d_3.

It is well-known conjecture that the real traveling wave speed correspond to the minimun speed of (11). That is, the traveling wave speed c will be equal to $2\sqrt{d_2(\varepsilon - \alpha_2\bar{p})}$. In fact, we examine the speed by using numerical simulations and check the speed of traveling wave which is equal to $2\sqrt{d_2(\varepsilon - \alpha_2\bar{p})}$. For instance, we carry out numerical simulations with $d_2 = 0.5$ and $d_2 = 2$(Fig.3) and the other parameter values as the following:

$$\varepsilon = 1 \quad \alpha_1 = \alpha_2 = 2, \quad \beta_1 = 2, \quad \gamma = 1.$$

Figure3 show that the speed in the case of $d_2 = 0.5$(red line), $c = \Delta x/\Delta t \approx 1$, and the speed in the case of $d_2 = 2$ (blue dots) is twice of the case $d_2 = 0.5$.

Therefore, we have the traveling wave solution which moves with the speed depending on the diffusion coefficient d_2 of invader prey but not d_1 and d_3. As one of numerical simulation results, Figure 4 show that the speed c is proportional to $\sqrt{d_2}$ but constant to d_3.
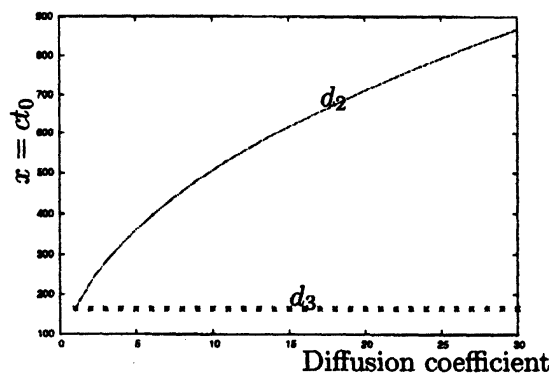

Figure 4: Dependence of diffusion coefficients d_2 and d_3

4 Conclusions

In this paper, we have shown that three species are able to coexist and diffuse with constant speed. Moreover, the diffusion speed depends only on the diffusion coefficient of the invader prey. The invasion of the invader prey lead the predator's population to increase. Furthermore, the remains of carcass of the invader prey also change the existent prey's population. We can suppose that the effect of the invader prey's population is very large at the head of traveling wave. Moreover, we have seen chaos in the diffusion model (3). The diffusion effect may give more complex fluctuation of populations.

Until now, many prey-predator population models have been studied but usually, they have not considerd the existence of carcass. However, it is very important that the remains of carcass of some species effects the population of outsider preys as well as themselves. In this paper, we have only considered the one predator case but we should consider the case of more than one predator for the remains of carcass. Moreover, we should also study about the effect of remains of carcass with different functional responses.

References

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[3] Tanabe K., Namba T., Omnivory creates chaos in simple food web models. Ecology, 86(2005) 3411-3414