An exploitation–competition system with negative effect of prey on its predator

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ABSTRACT

This paper considers an exploitation–competition system in which exploitation is the dominant interaction when the prey is at low density, while competition is dominant when the prey is at high density due to its negative effect on the predator. The two-species system is characterized by differential equations, which are the combination of Lotka–Volterra competitive and predator–prey models. Global dynamics of the model demonstrate some basic properties of exploitation–competition systems: (i) When the growth rate of prey is extremely small, the prey cannot promote the growth of predator. (ii) When the growth rate is small, an obligate predator can survive by preying on the prey, while a facultative predator can approach a high density by the predation. (iii) When the growth rate is intermediate, the predator can approach the maximal density by an intermediate predation. (iv) When the growth rate is large, the predator can persist only if it has a large density and its predation on the prey is big. (v) Intermediate predation is beneficial to the predator under certain parameter range, while over- or under-predation is not good. Extremely big/small predation would lead to extinction of species. Numerical simulations confirm and extend our results.

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1. Introduction

The dynamical framework of Lotka–Volterra models has formed the backbone of ecological modeling. In the Lotka–Volterra predator–prey model, the prey provides food and other resources for predator and promotes its growth, while the predator benefits from the prey and does it no good. The effect of one species on the other is either positive or negative without sign change. In real situations, the effect may be changeable. For example, the prey can have a negative effect on predator when at high density [12,23,25]. Thus the Lotka–Volterra predator–prey model should be expanded to characterize the changeable interaction, which exhibits exploitation when at low density but competition at high density. The exploitation–competition interaction has been observed in real situations for years.

Exploitation–competition interactions widely exist in animal systems. As shown by Polis et al. [16], rattlesnakes are food of adult burrowing owls, while the snakes eat eggs and nestlings of the owls. When the snakes are at low density, their net effect on the owls is positive and exploitation is the dominant interaction. However, when the snakes are at high density, the net effect becomes negative since more eggs and nestlings are eaten and the growth rate of the owls is reduced, and competition is the dominant interaction. Thus the

interactions between the rattlesnakes and owls are density-dependent and in the form of exploitation–competition. The second example occurs in the system of ctenophores and fish [3,17]: the ctenophores are food of adult fish, while they prey on the eggs and larvae of these fish. In another study, Barkai and McQuaid [2] showed that whelks are food of rock lobsters while they may overwhelm and consume the lobsters when they are in high abundance. As a final example, we cite the situation shown by Dayton [4]: "Copepods are important predators on the larvae of fish that, should they survive, become important predators on copepods. Indeed it is reasonable to imagine that small plankters such as copepods, euphausids, chaetognaths, etc, are important predators on even very large carnivores such as tuna. A terrestrial analogy would involve the spectre of say, tigers or wolves releasing thousands of tiny tigerlets or wolflets, which were largely consumed by spiders, lizards, birds, shrews, etc." For more relevant works, we refer to Schaller [18,19], Margalhães et al. [15], Hernandez [8], Kang and Wedekin [11], etc. While age-structured models have been used to describe the systems, expanded Lotka–Volterra models can demonstrate underlying mechanisms.

In plant–animal systems, there exist examples of exploitation–competition interactions. As shown by Zhong et al. [27], grass is the main food of herbivorous Brandt's vole in an Inner Mongolian grassland in China. However, when the grass is at high density, it also acts as an obstacle for these small herbivores to interact and communicate. Thus the voles' mating opportunity is reduced and their growth rate is decreased. Therefore, exploitation is the dominant interaction

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between the grass and herbivores when the grass is at low density, while competition is dominant when the grass is at high density.

Besides this direct negative effect of prey on its predator, there is an indirect negative effect, as shown in experiments by Urabe and Sterner [24]. In their experiments involving zooplankton and phytoplankton, algae was grown in batch cultures and zooplankton grazed on the algae. Light energy and carbon could freely enter the system from air as CO_2, and light intensity could be changed to different levels. The nutrient phosphorus was limited while other nutrients were abundant. When the light intensity was enhanced, algal density always increased monotonically, but the grazer's density exhibited different characteristic: as the light intensity was enhanced from low levels to intermediate levels, both of the algal and grazer's densities increased; however, as the intensity was enhanced from intermediate levels to high levels, the algal density increased but the grazer's density decreased. This paradoxical result in energy terms was explained by Urabe and Sterner [24] through stoichiometry of two elements, carbon and phosphorous. Here, stoichiometry denotes "that branch of the science which concerns itself with material transformations, with the relations between the masses of the components" [14].

The explanation of Urabe and Sterner [24] can be briefly shown as follows. In the experiments mentioned above, algal density increased by enhancing photosynthetic fixation of carbon when light intensity was high. Since the nutrient phosphorus in the system was limited, the phosphorus:carbon (P:C) ratio in algal biomass decreased. However, the grazer must maintain a specific P:C ratio in its body [1,22]. If the P:C ratio in algal biomass is lower than the specific value, the grazer cannot consume the excess carbon obtained from algae and has to excrete it. Thus, the algae growing at high light intensity became low-quality resource, which led to decrease of the grazer. Here, there exists a critical algal density (i.e., a critical light intensity), above which the P:C ratio in algal biomass is less than the specific value acquired by the graze and the algae has negative effect on its grazer. Therefore, indirect competition between algae and its grazer for phosphorus could result in transition of algae–grazer interactions from predation to competition. For more relevant works, we refer to Elser et al. [5–7], Sterner [20], Sterner et al. [21,22], etc.

Several researches have been focused on exploitation–competition interaction. Holland and DeAngelis [10] made consumer–resource models to characterize the exploitation–competition interactions between animals. Numerical simulations demonstrated that varying one parameter or population density of species could lead to transitions of interaction outcomes between predation $(+-)$ and competition $(--)$ in a smooth fashion. Loladze et al. [13] constructed a two-dimensional Lotka–Volterra type model to describe the algae–zooplankton system studied by Urabe and Sterner [24]. It was assumed that the P:C ratio in algal biomass never falls below a minimum and that the P:C ratio in grazer's biomass maintains a constant value. Thus, the growth of both algae and its grazer depends upon energy flow and element cycling. Theoretical analysis on the model exhibited that indirect competition between the two species for phosphorus could lead to transition of interaction outcomes from predation $(+-)$ to competition $(--)$. This competition can even lead to extinction of the grazer. Moreover, numerical simulations showed that the paradox of energy enrichment could occur when the grazer is phosphorus limited. While these models exhibit interesting features of exploitation–competition interaction, most of them are rather complicated such that global dynamics of the models cannot be shown as clearly as those of Lotka–Volterra predator–prey model. Thus, forming an appropriate model and demonstrating basic properties of exploitation–competition interaction is necessary.

In this paper, we consider an exploitation–competition model, which is the Lotka–Volterra predator–prey model when prey is at low density and is the Lotka–Volterra competitive model when prey is at high density. Theoretical analysis demonstrates some basic properties of exploitation–competition systems.

2. Model

In this section, we consider an exploitation–competition model in which the two-species interaction is in exploitation when the prey is at low density, while it is in competition when the prey is at high density. The model is depicted by

$$\frac{dx}{dt} = x(r_1 - d_1 x - a_{12} y),$$
$$\frac{dy}{dt} = y[-r_2 + a_{21}x_0 - a_{21}f(x) - d_2 y], \qquad (2.1)$$

where x and y represent population densities of the prey and predator, respectively. All parameters (except r_2) in the system are positive. In the first equation of (2.1), r_1 denotes the intrinsic growth rate of the prey, and r_1/d_1 represents its carrying capacity when in isolation from the predator. The parameter a_{12} denotes the strength of predation. We denote isocline $l_1 : r_1 - d_1 x - a_{12} y = 0$, and function $g_1(x, y) = x(r_1 - d_1 x - a_{12} y)$.

In the second equation of (2.1), the function $f(x) = |x - x_0|^*$ is defined as the absolute function $|x - x_0|$ while the function $y = |x - x_0|$ is smoothed in a very small neighborhood of its vertex $(x_0, 0)$. When $x_0 = 0$, we have $dy/dt = y(-r_2 - a_{21}x - d_2 y)$. Thus, $-r_2$ is the per-capita mortality (resp. growth) rate of the predator when $-r_2 < 0$ (resp. $-r_2 > 0$), which corresponds to obligate predation (resp. facultative predation). d_2 represents the degree of intraspecific competition among predators, while a_{21} represents the negative effect of prey on the predator. We focus on solutions of (2.1) with $x(0) > 0$, $y(0) > 0$, thus we have $x(t) > 0$, $y(t) > 0$ as $t > 0$.

Denote $L_2(x, y) = -r_2 + a_{21}x_0 - a_{21}f(x) - d_2 y$. Thus the isocline $l_2 : L_2(x, y) = 0$ consists of l_{21} and l_{22}, as shown in Fig. 1. Since the function $g_2(x, y) = yL_2(x, y)$ is smooth and satisfies

$$\frac{\partial g_2}{\partial x} = a_{21}y > 0 \quad \text{as} \quad x < x_0,$$
$$\frac{\partial g_2}{\partial x} = -a_{21}y < 0 \quad \text{as} \quad x > x_0,$$

the prey has a positive effect on the predator when it is at low density $(x < x_0)$, but has a negative effect on the predator when at high density
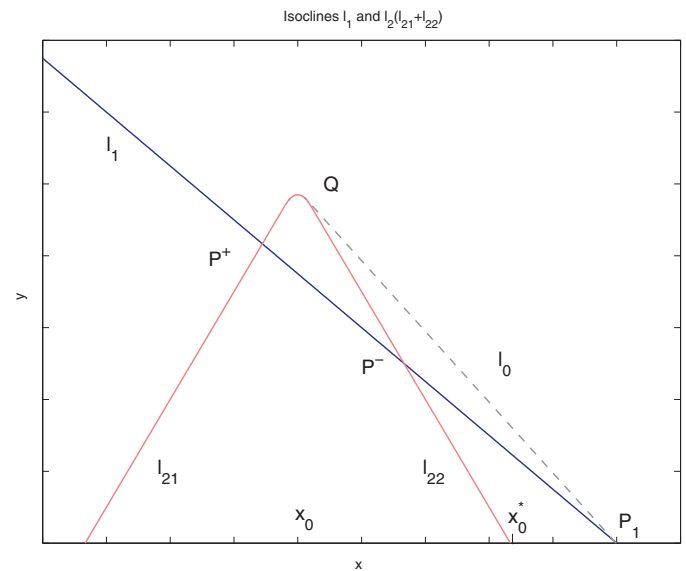

Fig. 1. Isoclines l_1 and l_2 as $r_2 > 0$, while l_2 consists of l_{21} and l_{22}. l_1 and l_2 are represented by blue and red lines, respectively. Q is the vertex of l_2 and P_1 is the intersection point of l_1 and the x-axis. l_0 is a line connecting Q and P_1, which is denoted by dashed line. l_1 and l_2 intersect at two points: l_1 and l_{21} intersect at P^+, while l_1 and l_{22} intersect at P^-. x_0 and x_0^* are important values defined in Section 3 of this work. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)