Effects of additional food in a delayed predator–prey model

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ABSTRACT

We examine the effects of supplying additional food to predator in a gestation delay induced predator–prey system with habitat complexity. Additional food works in favor of predator growth in our model. Presence of additional food reduces the predatory attack rate to prey in the model. Supplying additional food we can control predator population. Taking time delay as bifurcation parameter the stability of the coexisting equilibrium point is analyzed. Hopf bifurcation analysis is done with respect to time delay in presence of additional food. The direction of Hopf bifurcations and the stability of bifurcated periodic solutions are determined by applying the normal form theory and the center manifold theorem. The qualitative dynamical behavior of the model is simulated using experimental parameter values. It is observed that fluctuations of the population size can be controlled either by supplying additional food suitably or by increasing the degree of habitat complexity. It is pointed out that Hopf bifurcation occurs in the system when the delay crosses some critical value. This critical value of delay strongly depends on quality and quantity of supplied additional food. Therefore, the variation of predator population significantly effects the dynamics of the model. Model results are compared with experimental results and biological implications of the analytical findings are discussed in the conclusion section.

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1. Introduction

The traditional approach of modeling predator–prey interaction is often based on an organism's primary function within a food web (e.g., prey and predator). Additional food is an important component of most predators (e.g., coccinellid) diet, and although they receive less attention than prey in the scientific literature, these foods fundamentally shape the life histories of many predator species. The availability of suitable additional food (non-prey food) in a predator–prey system can have significant impact on the dynamics of the system. The consequences of providing additional food to predator and the corresponding effects on the predator prey dynamics and its utility in biological control (such as species conservation and pest management) have been a topic of great attention for many scientists. In recent years, many biologist, experimentalists, and theoreticians investigated the consequences of providing additional food to predators in predator–prey systems [1–8]. Huxel and McCann [2] investigated the impact of additional food on the stability of a simple food web model. Huxel et al. [3] proposed a food web model with variable allochthonous inputs which are either one type available to both consumer and predator or

two distinct types, one for consumer and one for predator. Srinivasu et al. [6] examined the qualitative behavior of a predator–prey system in presence of additional food to the predator. They concluded that handling times for the available foods to the predator play the key role in determining the dynamical behavior of the system. Haque and Greenhalgh argued that alternative food source may play an important role in promoting the persistence of predator–prey systems [9]. Guin et al. [10] investigated the significant role of self and cross-diffusion coefficients in a prey-dependent predator–prey model in which predator has alternative source of food. Recently, a chaos control mechanism of a predator–prey system incorporating additional food to predator is reported by Sahoo and Poria [5].

Habitat complexity is the structural complexity of habitats. Habitat complexity can strongly mediate predator–prey interactions, affecting not only total predation rates, but also modifying selectivities for different prey species or size classes [11–16]. Pennings [17] and Grabowski [18] found that habitat complexity reduces encounter rates of predators with prey. For example, aquatic habitat becomes structurally complex in presence of submerged vegetation or aquatic weeds. It is observed that structural complexity of the habitat stabilizes the predator–prey interaction between piscivorous perch (predator) and juvenile perch and roach (prey) by reducing predator foraging efficiency. Luckinbill prolonged the coexistence of *Paramecium aurelia* (prey) and *Didinium nasutum* (predator) in laboratory system by increasing strength of habitat complexity using

methyl cellulose in the Cerophyl medium (nutrient) [19]. Therefore, it is important to incorporate the effect of habitat complexity when predator–prey interaction is studied by means of theoretical models.

The models with delay are much more realistic, as in reality time delays occur in almost every biological situation [20–27]. It is more realistic to assume that the reproduction of predator after predating the prey will not be instantaneous, but mediated through some time lag which is required for gestation of the predator [28]. After predation, some amounts of energy in the form of biomass of prey assimilate into the predator's energy also in the form of biomass. But this bio-physiological process is not simple; the conversion of prey energy to predator energy is not instantaneous, and several processes are involved in this mechanism. Caperon [29] examined the *Isochrysis galbana* growing in a nitrate limited chemostat, over two experiments (one of 56 days and another of 80 days). He observed that there is a time delay between the changes in substrate concentration and the corresponding changes in the bacterial growth rate. So, inclusion of time delay will certainly make the predator–prey model one step closer to real situation.

Predators are predominantly valued for their ability to control prey and as a result to keep high levels of biodiversity. Effects of variation of predator population on the model are investigated. Additional food helps to control predator population in the model. Good quality or high quantity of additional food favor rapid growth of predator population. Majority of the predator–prey models has not incorporated the effects of habitat complexity as well as the effects of additional food in biological systems. The main goal of this paper is to investigate the role of additional food as a biological controller in a delayed predator–prey system with habitat complexity. The organization of the paper is as follows: We propose a food chain model incorporating effects of additional food to predator in Section 2. In Section 3 the existence conditions of interior equilibrium point are derived and role of additional food on the existence conditions are reported. Effects of additional food on the stability condition of the interior equilibrium point is derived. Role of additional food on the stability and direction of periodic solutions are investigated by using the normal form theory and the center manifold theorem due to Hassard in Section 4. Numerical simulation results are supplied in Section 5 in support of the theoretical analysis. Finally conclusion is drawn in Section 6.

2. The model

We shall now derive the modified form of functional response considering the effects of additional food to predator with habitat complexity. The rate of prey consumption by an average predator is known as the functional response. This can be classified as: (a) prey dependent, when prey density alone determines the response; (b) predator dependent, when both predator and prey populations affect the response; and (c) multi-species dependent, when species other than the predator and its prey species influence the functional response [30]. The most commonly used functional response in a predator–prey model is the Holling Type-II functional response [31]. The Holling type-II functional response is defined as

$$f(x) = \frac{ax}{1 + ahx},$$

where $f(x)$ is the amount of food consumed, x is the amount of food offered, a is a proportionality constant related to the attack rate, h is the handling time per food item. Since the existence of habitat complexity reduces the probability of capturing a prey by reducing the searching efficiency of predator and habitat complexity affects the attack coefficient [32]. Therefore, the attack coefficient a has to be replaced by $a(1 - c)$, where c ($0 < c < 1$) is a dimension less parameter that measures the degree or strength of habitat complexity. We assume that the complexity is homogeneous throughout the habitat. Then following Kot [33], the total number of prey caught(V), is given

by

$$V = a(1 - c)T_s x, \quad \text{where} \quad T_s = T - hV.$$

Here T is the total time, T_s is the available searching time. Solving for V we get the modified Holling type-II response function as

$$V = \frac{Ta(1 - c)x}{1 + a(1 - c)hx}.$$

Since, predator's functional response is defined as the number of prey caught by a predator at unit time, so the functional response in presence of habitat complexity is given by

$$f(x) = \frac{a(1 - c)x}{1 + a(1 - c)hx}.$$

The term c ($0 < c < 1$) measures the strength of habitat complexity, which reduces the predation rate. Notice that for $c = 0$, there is no complexity, we get the original Holling Type II response function.

Assuming density-dependent logistic growth of prey with intrinsic growth rate r, the predator–prey model is of the form

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - \frac{a(1 - c)xy}{1 + a(1 - c)hx} = rx\left(1 - \frac{x}{k}\right) - f(x)y,$$

$$\frac{dy}{dt} = \frac{\theta a(1 - c)xy}{1 + a(1 - c)hx} - dy = g(x)y - dy, \quad (1)$$

where x denotes the density of prey, y is the density of the predator, k is the carrying capacity of the prey in ecosystem, θ is the conversion efficiency of prey into the predator and d is the mortality rate of predator.

One aspect of habitat manipulation is the addition of floral resources to agro-ecosystems to provide additional food to predators, potentially enhancing their fitness and efficacy [34,35]. These techniques could also be used to improve the success of classical biological control attempts [36]. The mirid predator *Macrolophus pygmaeus* is a natural enemy of major economic importance for the control of white flies and other small arthropod pests in Europe [37–40]. It is observed that provision of a minimum of 40 eggs per individual predator for three days is required for optimal development and reproduction of this mirid predator. Providing the predator with lower quantities of eggs resulted in higher mortality, slower development and lower adult weights [40]. Since provision of eggs to the predator proved expensive, experiments were conducted to find if pollen can be a supplementary food for this predator [40]. It is observed that food consisting of 10 eggs and 15 mg of pollen was needed for optimal development of the predator, which was relatively a cheaper alternative [40,41]. Thus availability of additional food of a fixed quality appears to be vital in the development, conservation and sustainability of the species both ecologically and economically. Both theoretical studies [6] and experimental results [42–44] established that provision of additional food to predators mediates indirect interactions between the species of the ecosystem, ultimately affecting the population dynamics of the predator and prey. The above fact motivate us to incorporate effects of additional food in our model.

We now modify the model (1) by supplying "additional food" [6,8] to predator. The predator is provided with a constant additional food in case of extinction of the prey as predator has alternate source of food other than the prey available to it. We make the following assumptions:

(a) The predator is provided with additional food of constant biomass A which is assumed to be distributed uniformly in the habitat. The constant biomass assumption is valid for many arthropod predators because they can feed on plant-provided alternative food sources such as pollen or nectar which approximately remains constant [1]. Therefore, the predator is a generalist with a resource other than the prey available to it.

(b) The number of encounters per predator with the additional food is proportional to the density of the additional food. The