



Original Research Article

Foraging facilitation among predators and its impact on the stability of predator–prey dynamics



Lenka Přibyllová*, Anna Peniašková

Department of Mathematics and Statistics, Section of Applied Mathematics, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic

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ABSTRACT

Predator foraging facilitation may strongly influence the dynamics of a predator–prey system. This behavioral pattern is well-observed in real life interactions, but less is known about its possible impacts on the predator–prey dynamics. In this paper we analyze a modified Rosenzweig–MacArthur model, where a predator-dependent family of functions describing predator foraging facilitation is introduced into the Holling type II functional response. As the general assumption of foraging facilitation is that higher predator densities give rise to an increased foraging efficiency, we model predator facilitation with an increasing encounter rate function. Using the tools of bifurcation analysis we describe all the nonlinear phenomena that occur in the system provoked by foraging facilitation, these include the fold, Hopf, transcritical, homoclinic and Bogdanov–Takens bifurcation. We show that foraging facilitation can stabilize the coexistence in the predator–prey system for specific rates, but in most of the cases it can have fatal consequences for the predators themselves.

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1. Introduction

Behavioral interaction among the entities of predator or prey populations, both positive and negative, may change and modify the basic findings of population biology and theory of ecology and may also have a substantial effect on the individual's foraging success (Skalski and Gilliam, 2001). The importance of the inclusion of predator behavior into the predator–prey interaction models has been recognized (e.g. Abrams and Ginzburg, 2000; Arditi and Akcakaya, 1990; Lima, 2002) but little is known about the nonlinear phenomena that may appear in predator–prey systems with interaction due to bifurcations. Empirical studies and observations have shown the presence of interacting behavior in animal populations; lions or baboons are very often subjects of such observations (Heinsohn and Packer, 1995). Interacting predator–prey systems especially with cooperative or foraging behavior are often modeled as a social dilemma in game theory

with several strategies of behavior to adopt (Iwasa, 1982; Packer and Ruttan, 1988; Brown et al., 1999; Doebeli and Hauert, 2005). The motives and evolution even of human cooperative behavior is not thoroughly known currently; Richerson and Boyd (2001) argue that deeper understanding of human behavior may lead to a better explanation of other species.

Predator functional response, that is, the per capita feeding rate of predators upon their prey, is a basic concept in the predator–prey theory from its beginning. There is a variety of functional response types, almost every textbook (e.g. Begon et al., 1990; Krebs, 2001) refers to the traditional classification of the three density-independent types (Holling, 1959): Holling type I (linear), Holling type II (concave increase) and Holling type III (sigmoid increase) functional responses. There is a wide range of different functional relations of feeding rate with respect to the predator population density (Skalski and Gilliam, 2001). The most illustrative choices are an increasing or a decreasing feeding rate. One may interpret the decreasing feeding rate as a predator population where the entities interfere. Predator interference is a collective term that includes a number of specific mechanisms from stealing subdued prey to mechanisms connected with territorial behavior

* Corresponding author.

E-mail address: pribyllova@math.muni.cz (L. Přibyllová).

of the predator or the prey. There is a wide range of literature available on interference, such as (Arnqvist et al., 2006; Ruxton et al., 1992; Ruxton, 1995).

Increasing feeding rate, on the other hand, represents foraging facilitation among the entities of the predator population. Although foraging facilitation is the opposite process to predator interference, contemporary predator–prey theory often overlooks this aspect despite the fact that an inclusion of the facilitation in ecology theory may influence the results and the learnings gained so far in predator–prey theory (Giraldeau and Caraco, 2000; Bruno et al., 2003). Foraging facilitation can manifest in different ways, it can be an ability to locate or capture the prey in a bigger group (Cosner et al., 1999), intraspecific cooperation (Courchamp and Macdonald, 2001), protecting mechanisms against other species (Krause and Ruxton, 2002), or accessibility of public information on the availability of food (Bijleveld et al., 2015).

Recent studies devoted to density dependent functional responses and their effects on predator–prey dynamics (e.g. Nilsson et al., 2006; Fryxell et al., 2007; Boukal et al., 2008; Berec, 2010; Přibyllová and Berec, 2014) show that density dependent functional responses bring about new stabilizing and destabilizing mechanisms of predator–prey dynamics. The aim of the present paper is to build on the findings of Berec (2010) and Přibyllová and Berec (2014) and analyze these mechanisms for a family of functional responses representing positive interaction among the entities of the predator population. While Berec (2010) gives a brief overview on the number and the character of the coexistence equilibria, we present a complete and thorough analysis of the system with foraging facilitation. In Berec (2010), Berec calls for further, more detailed studies on the models with predator facilitation and interference, with special attention on the limit cycle behavior. A step towards the understanding of the phenomena that may occur in systems with interacting predators was the analysis of interfering predators in Přibyllová and Berec (2014). However, the picture is not complete without the predator facilitation case, which is the question we address in the recent paper. While the notation is similar to that in Přibyllová and Berec (2014), the approach of our analysis is different and so are our findings. We have considered the family of functional responses suggested in Berec (2010) with unbounded above encounter rate and a more realistic family of functional responses with bounded above encounter rate. The latter corresponds with the findings of several empirical studies (Bijleveld et al., 2015) and studies on game theory models (Packer and Ruttan, 1988). While Berec (2010) considers only the number and character (i.e. stability) of the coexistence equilibria, our analysis goes deeper and examines the bifurcations that may occur. We concentrate on the conditions of appearance of multi-stable regions.

Observations of cooperative behavior, mainly cooperative hunting, have been published several times (Packer and Ruttan, 1988; Creel and Creel, 1995; Heinsohn and Packer, 1995). A general rule of cooperative hunting strategy is that the benefits of group hunting for each hunter have to outweigh the benefits of solitary hunting. Packer and Ruttan (1988) showed that cooperative hunting can be the evolutionarily stable strategy for species hunting a single small prey, a small group size of the hunters hunting a single large prey, or for a large group of hunters hunting multiple large preys. Species with cooperative hunting strategy have an increasing above bounded hunting success function with respect to the hunter group size. Packer's findings validate the consideration of an increasing above bounded encounter rate at least for several specific predator–prey populations (such as lions and hyenas).

The analyzed model is a modification of the classic Rosenzweig–MacArthur predator–prey model (Rosenzweig, 1971) with Holling type II functional response of predators. The

Rosenzweig–MacArthur model demonstrates the paradox of enrichment where stable oscillations bifurcate out of a stable equilibrium once the environmental carrying capacity of the prey exceeds a critical value (Kot, 2001). We show that our model keeps this very typical behavior after the encounter rate functions for foraging facilitation are introduced. Another destabilization may appear due to the homoclinic bifurcation that causes splitting of the stable cycle, thus ending the oscillations and consequently causing the extinction of the predators. This phenomenon influences the prey density as well.

2. Model

2.1. Generic model with predator foraging facilitation

Let us consider the following modified Rosenzweig–MacArthur predator–prey model with the predator-dependent functional response

$$\begin{aligned}\frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) - Pf(N, P), \\ \frac{dP}{dt} &= ePf(N, P) - mP.\end{aligned}\quad (1)$$

In this model, N and P are prey and predator densities, respectively, r is the intrinsic per capita growth rate of the prey, K is the environmental carrying capacity of the prey, m is the per capita predator mortality rate, and e is the efficiency with which the consumed prey is transformed into new predators. The density of the prey increases logistically in the absence of the predator, while the predator dies out exponentially in the absence of the prey. The predator functional response $f(N, P)$ is a generalized Holling type II functional response with the predator encounter rate λ being a smooth and increasing function of the predator density P

$$f(N, P) = \frac{\lambda(P)N}{1 + h\lambda(P)N}, \quad (2)$$

where $\lambda(0) \geq 0$, $\lambda'(P) > 0$, and h denotes the predator handling time of one prey. The general assumption of foraging facilitation is that higher predator densities give rise to an increased foraging efficiency and hence increase encounter rate for any member of the foraging party.

Combining the generic model (1) with the functional response (2), our primary model is

$$\begin{aligned}\frac{dN}{dt} &= rN \left(1 - \frac{N}{K}\right) - \frac{\lambda(P)N}{1 + h\lambda(P)N}P, \\ \frac{dP}{dt} &= e \frac{\lambda(P)N}{1 + h\lambda(P)N}P - mP.\end{aligned}\quad (3)$$

2.2. Specific models

Berec (2010) considers a specific encounter rate function

$$\lambda(P) = \lambda_0(b + P)^w, \quad (4)$$

where $b \geq 0$, $\lambda_0 > 0$. For a positive w , $\lambda(P)$ is increasing. Encounter rate (4) is an increasing unbounded above function, concave for $w \in (0, 1)$ and convex for $w > 1$. Note that for $w < 0$, encounter rate (4) models a negative interaction. Varying w in (4) produces a family of functional responses, whereas varying b or λ_0 does not qualitatively change the functional response. Substituting $b = 0$ and $\omega = -w$ into (4) leads to the Hassel–Varley functional response

$$f(N, P) = \frac{\lambda_0(N/P^\omega)}{1 + h\lambda_0(N/P^\omega)}. \quad (5)$$

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