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Predator interference emerging from trophotaxis in predator–prey systems: An individual-based approach

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ABSTRACT

An individual-based model describing predator–prey interactions within a closed rectangular habitat was developed to study how different assumptions about the individual movements lead to the emergence at the population level of various kinds of prey- and predator-dependence in the spatially aggregated trophic function.

In addition to random walk, both species are capable of directional movement, i.e., the model accounts for the predator prey-taxis and evasion of predators by prey individuals. The taxis stimulus of each species is the odour of the other species, which is distributed continuously in space. Spatial behaviour of individuals is determined by the specific response to the odour gradient and the tendency to maintain the taxis velocity.

In order to facilitate the assessment of the trophic function, the model allows removing the effect of demographic density variations on the predator ration, keeping population sizes constant.

Analyzing the dependence of the trophic function with the average predator density, we found that, depending on the intensity of taxis, the predator population exhibits various degrees of interference, from very low to very high values. In particular, a moderate taxis generates distinct levels of interference including the ratio-dependent case. The letter maximizes the average consumption rate.

A new generalized function containing ratio-dependence and prey-dependence as special cases, at high and low population abundances, is suggested. This trophic function fits the simulated data better than the Hassell–Varley–Holling expression does.

1. Introduction

Paradoxically, for the past 70 years, the key element of predator–prey models, i.e., the quantification of the rate of predation of prey by predators, is a source of controversy. The essence of the debate is the question that was first raised by Volterra (1931), about the effect that predator population abundance could have on the individual rate of consumption. Different answers to this question can alter significantly the dynamic properties of mathematical models, their predictions about community dynamics and response to external impacts.

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Formally, the problem consists in quantifying the amount of prey consumed per predator per unit time (i.e., the individual predator ration, g) in dependence on population abundances. The functional form of this dependence, i.e., the trophic function (named also 'functional response') may be different, having either prey-dependent [$g = g(N)$] or predator-dependent [$g = g(N,P)$] forms, where N and P are the prey and predator population abundances, respectively (Arditi and Ginzburg, 1989). Hereafter, in order to distinguish local population densities from those averaged over the whole area, we use the term 'population abundance' as a synonym to 'spatially averaged population density'.

Since the classical works of Lotka (1925) and Volterra (1926), the conventional theory of trophic relations has been based on the mass action principle, assuming that predators encounter prey at random. This assumption leads to prey-dependent trophic functions. In homogeneous well-mixed systems, prey-dependent models seem theoretically justified and have been validated by some experiments in small-scale laboratory microcosms (Gause, 1935; Holling, 1959; Luckinbill, 1973; Veilleux, 1979; Arditi and Saïah, 1992; Bohannan and Lenski, 1997, 1999; Haydon and Lloyd, 1999; Jeschke et al., 2004; Tully et al., 2005). However, the hypothesis of prey-dependence fails to describe the dynamics of large-scale natural trophic systems, leading to numerous inconsistencies between model predictions and observations (Arditi and Ginzburg, 1989; Arditi and Akçakaya, 1990). Generally speaking, prey-dependent trophic functions do not allow reproducing the real dynamics of interacting populations in the framework of non-spatial (point) mathematical models. Particularly, this is the case of the 'top-down' and 'cascading' theories as well as of the well-known 'paradoxes' of biological control and enrichment (Rosenzweig, 1971; Oksanen et al., 1981; Luck, 1990; Arditi and Berryman, 1991; Berryman, 1999; Skalski and Gilliam, 2001). Modifying the trophic function, accounting for its dependence on predator abundance leads to the resolution of the contradictions between theory and natural observation phenomena.

To date, various theoretical functions of both prey-dependent and predator-dependent types exist; some are presented in Table 1. Parameters in these formulas are positive coefficients: a is the searching efficiency; h is the handling time; $g_{\max}$ is the maximum individual ration; s is the predation efficiency, τ is the length of the consumption bout; m and b quantify predator interference. In all these functions, the individual predator ration $g(N,P)$ increases monotonically with N and either decreases with P [predator-dependence] or does not depend on P [prey-dependence].

The empirical evidence for an adverse influence of predator abundance on the predator ration was first given by Hassell and Varley (1969) on the basis of data on insect predators and parasitoids. Both the BDA and the HVH expressions provide generalized representations with variable intensity of predator-dependence. In the present paper, we will focus on the HVH trophic function because it is rather versatile, coinciding in special cases with the prey-dependent Holling type II ($m = 0$), the Lotka–Volterra ($m = 0$, $h = 0$), the Hassell–Varley ($h = 0$) and the Arditi–Ginzburg ratio-dependent ($m = 1$) trophic functions. Note that in the HV and HVH models the searching efficiency depends inversely to the power of the predator density P: $a = \alpha/P^m$. Since this expression is dimensionally unbalanced, a more correct formula is $\alpha(P_0/P)^m$, where P_0 is the density of a 'population' consisting of a single predator, and which can always be scaled so that $P_0 = 1$ by an appropriate choice of spatial units. Thus, when $m > 0$, the coefficient α is not the standard 'searching efficiency' as in the Holling model but it must be, strictly speaking, understood as the searching efficiency of a single predator unaffected by competitors. The dynamics of predator–prey models incorporating the HVH trophic function was studied by Arditi and Akçakaya (1990) and Arditi et al. (2004).

Recently Trần (2008) has analytically derived new forms of predator-dependent trophic functions that are hybrid between linear ratio-dependent $g(N,P) = \alpha N/P$ and Lotka–Volterra expressions (see Table 1). These functions illustrate the challenging idea formulated by Ginzburg and Jensen (2008) that a general trophic function should ideally exhibit both prey-dependent and predator-dependent properties, according to the population densities. In particular, predator-dependent functions suggested in (Trần, 2008) approach the ratio-dependence with increase of predator abundance.

Predator-dependence is often explained as a consequence of spatial heterogeneity (see, e.g., Bergström et al., 2006) and spatial behaviour of populations (e.g., Cosner et al., 1999). Non-random search, i.e., the tendency of predators to aggregate in prey patches, their ability to display directional movement (e.g., prey-taxis as a particular case of tropho-taxis), prey grouping, and group hunting of predators are the most important behavioural mechanisms that induce spatial heterogeneity and affect the predator ration at the population level (Free et al., 1977; May, 1978; Sutherland, 1983; Chesson and Murdoch, 1986; Arditi and Ginzburg, 1989; Arditi and Akçakaya, 1990; Hassell, 2000; Vucetich et al., 2002). In other words, non-spatial (point) predator–prey models that incorporate predator-dependent trophic functions, account *implicitly* for various spatial aspects of population dynamics. Although they demonstrate realistic dynamic properties and provide better fits to data in cases where prey-dependent models fail (Arditi and Saïah, 1992; Jost and Ellner, 2000; Skalski and Gilliam, 2001), models with predator-dependent functional responses are often phenomenological: postulating the dependence of the trophic function on predator population abundance, they do not explain the micro-scale mechanisms that lead to the emergence of predator-dependence on the larger spatio-temporal scale. Therefore, the theory of predator-dependence also requires building and studying *spatially explicit* mathematical models able to explain the appearance of predator-dependence on the global scale by mechanistic derivation or by considering the averages of dynamics over space (Blaine and DeAngelis, 1997; Poggiale et al., 1998; Bernstein et al., 1999; Cosner et al., 1999; Arditi et al., 2001).

Cosner et al. (1999) proposed a unified mechanistic approach to the derivation of various forms of trophic functions. Combining the principle of mass action with different hypotheses about clustering patterns of individuals, they showed how spatial averaging can produce several of the trophic functions of Table 1. However, assuming highly idealized behaviour rules and spatial shapes of clusters, this