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The DeAngelis–Beddington functional response and the evolution of timidity of the prey

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HIGHLIGHTS

- We study the evolution of “timidity” of the prey in a predator–prey model.
- A constant predator–prey population favors always less timidity.
- Low levels of timidity, however, may destabilize the population and lead to cycles.
- Population cycles of large amplitude favor a positive level of timidity.
- If such cycles do not occur, timidity evolves all the way to zero.

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ABSTRACT

We study the evolution of “timidity” of the prey (i.e., its readiness to seek refuge) in a predator–prey model with the DeAngelis–Beddington functional response. Using the theory of adaptive dynamics, we find that a predator–prey population at equilibrium always favours less timidity. Low levels of timidity, however, may destabilise the population and lead to cycles. Large-amplitude cycles favour a positive level of timidity, but if such cycles do not occur, timidity will evolve all the way to zero, where the prey no longer responds to the predator by seeking refuge, and in which case the DeAngelis–Beddington functional response has become identical to the Holling type–II functional response.

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1. Introduction

A basic ingredient of every predator–prey model is the predator's functional response, which is defined as the expected number of prey captured per unit of time by a single predator. The functional response is a consequence of the individual behaviour of the predator, the prey, or both the predator and the prey. For example, the Holling type–II functional response

$$F(x) := \frac{ax}{1+ahx}, \quad (1)$$

in which x denotes the prey population density, can be derived using a time-budgeting argument where the predator divides its time between searching prey and handling (i.e., killing, eating and digesting) of captured prey (Holling, 1959). Alternatively, the Holling type–II functional response can be derived from an explicit model of transitions between the individual states “handling” and “searching” on a time scale that is short compared to that of birth and death (Metz and

Diekmann, 1986, pp. 6–7). The two derivations are essentially equivalent, and in both cases the parameters a and h denote the same, namely, the rate of finding individual prey and the expected handling time per captured prey, respectively. These two parameters characterise the behaviour of the predator.

As a second example more directly relevant to the present paper, we consider the DeAngelis–Beddington functional response, independently proposed by DeAngelis et al. (1975) and Beddington (1975), and given by

$$F(x, y) := \frac{ax}{1+ahx+by}, \quad (2)$$

where x and y are the population densities of the prey and of the predator, respectively. This functional response can be derived if, in addition to Holling's assumption of searching and handling predators, we assume that only foraging prey can be captured, while prey that is hiding or that have become aware of the presence of the predator are safe (Geritz and Gyllenberg, 2012). The parameters a and h denote the same as in the Holling type–II functional response (1). The parameters b and τ denote, respectively, the rate at which the prey detects an individual predator (prompting it to hide or to

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become alert) and the expected time an individual prey stays hidden or stays alert before resuming foraging again. These two parameters characterise the behaviour of the prey. Notice in particular that if b or τ become zero, the DeAngelis–Beddington functional response turns into the Holling type–II functional response.

The question how the functional response evolves as a consequence of natural selection acting on the behaviour of the individuals themselves, can only be meaningfully addressed if the functional response is known in terms of the parameters that characterise the behaviour of the individual prey and predator. In this paper we study the evolution of the DeAngelis–Beddington functional response (2) when selection acts on the parameters b and τ . The product $b\tau$ will be referred to as the “timidity” of the prey: the higher the timidity, the higher the inclination of the prey to stop foraging and hide or become alert in response to the predator, or the longer it takes before the prey resumes foraging again, or both.

The adaptive advantage of hiding or being in a state of increased alertness in the presence of a predator is obvious because it lowers the risk of predation. But there is also a disadvantage: if prey do not forage while hiding or just being watchful, then the average *per capita* foraging rate of the prey will decline. Consequently, provided the prey birth rate is limited by its feeding rate, there is bound to be a trade-off with the average *per capita* birth rate of the prey. If indeed the birth rate is limited by the foraging rate, then such a trade-off will exist even if births occur at moments when the prey are not actually foraging. There are of course situations where foraging is possible also inside the refuge, but that is not the kind of situation that we consider: here the refuge is like a tree for an animal that normally feeds on the ground, or like an alerted animal that stops foraging to look around for stalking predators. Note that the trade-off between the timidity and the fecundity of the prey is apparent only because the functional response (2) is known in terms of the behaviour of the individual prey. Without this there would have been no reason to assume a connection whatsoever between the predator's functional response on the one hand and the fecundity of the prey on the other.

The aim of this paper is to find a level of timidity that balances the risk of predation against the loss of fecundity in a way that is favoured by natural selection. To this end, we first derive a multi-prey version of the DeAngelis–Beddington functional response for finitely many prey types that are all identical, except for their level of timidity. This multi-prey functional response is then used in a predator–prey model from which we derive invasion conditions for an initially rare prey type that is not present in the population yet. Using elements of the theory of adaptive dynamics (Metz et al., 1992; Geritz et al., 1997; Geritz et al., 1998), we find that selection in a constant predator–prey population always favours less timidity. The persistent decline of timidity, however, at some point may destabilise the population and lead to cycles. Only very large-amplitude cycles favour a positive level of timidity. If such cycles do not occur, timidity will evolve all the way down to zero, in which case the DeAngelis–Beddington (2) functional response becomes the same as the Holling type–II functional response (1), and the prey no longer responds to the presence of the predator.

The term “timidity” was first introduced in the context of predator–prey dynamics by Matsuda and Abrams (1994), who asked the same questions as we do, but who came to partially different conclusions. In the discussion section of this paper we will compare our results with theirs and explain the differences in terms of differences between the two models.

2. Multi-prey DeAngelis–Beddington functional response

Consider a population of $k \geq 1$ different prey types with timidities $b_1\tau_1, \dots, b_k\tau_k$. Each individual prey may be in one of two states:

“foraging” or “hiding”, where the latter may alternatively also refer to an elevated state of alertness. The population densities of prey in the respective states are denoted by x_i^F and x_i^H , and the total population density x_i of prey of type i is

$$x_i = x_i^F + x_i^H. \quad (3)$$

Likewise, the individual predator can be in one of two states: “searching” or “handling” with corresponding population densities y^S and y^H . The total population density y of the predator is

$$y = y^S + y^H. \quad (4)$$

For the individual prey, the transition rate from “foraging” to “hiding” is assumed to be proportional to the total population density y of the predator and denoted by $b_i y$. It could be argued that only an encounter with a searching predator should trigger the transition, because a handling predator is not an immediate danger to the prey. However, if the prey senses the predator by means of olfaction, sight or hearing from a distance at which the presence of an individual predator can be detected but not its state, then the transition rate will depend on the overall predator density rather than on the density of only searching predators (Geritz and Gyllenberg, 2012). The rate of a transition from “hiding” back to “foraging” is a constant τ_i^{-1} , where τ_i is the average hiding time for a prey of type i .

For the predator, a transition from “searching” to “handling” is triggered by an encounter with a foraging prey (the only kind of prey that can be captured), and so the transition rate, $a \sum x_j^F$, is proportional to the total population density of foraging prey, but it is otherwise independent of the type of prey. The rate of a transition from “handling” back to “searching” is a constant h^{-1} , where h is the average handling time.

We assume that transitions between the individual states are so much more frequent than the occurrence of births and deaths in the prey as well as in the predator, that we can consider the dynamics of the state transitions on a separate and faster timescale than that of the full population dynamics. On this faster timescale we have

$$\dot{x}_i^F = -b_i y x_i^F + \frac{1}{\tau_i} x_i^H - a y^S x_i^F, \quad (5)$$

$$\dot{y}^S = -a \left(\sum_{j=1}^k x_j^F \right) y^S + \frac{1}{h} y^H. \quad (6)$$

The term $-a y^S x_i^F$ in (5) represents death of prey by predation, which becomes negligible if we assume that the density of the predator is small relative to that of the prey. In addition, we then have to assume that the b_i is correspondingly large so that the term $-b_i y x_i^F$ does not vanish. In terms of the behaviour of the individual prey, this means that upon an encounter between a predator and a foraging prey, the latter is much more likely to escape by seeking refuge than to be captured by the predator. (A precise technical account of how to bring about the time-scale separation is given in Appendix A.)

The system of the four equations (3)–(6), but without the $-a y^S x_i^F$ term, has a unique and stable quasi-steady state

$$x_i^F = \frac{x_i}{1 + b_i \tau_i y}, \quad (7)$$

$$y^S = \frac{y}{1 + a h \sum_{j=1}^k x_j^F}. \quad (8)$$

Note that at the quasi-steady state, a proportion $(1 + b_i \tau_i y)^{-1}$ of the prey is actually foraging. This proportion is the same as the fraction of time individual prey spend foraging, and therefore can be interpreted as a measure of their foraging effort. This will

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