A mechanistic derivation of the DeAngelis–Beddington functional response

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HIGHLIGHTS

► We derive the DeAngelis–Beddington functional response in terms of behavior at the individual level.
► The derivation is based on a predator-induced change in individual state of prey from exposed to unexposed.
► The result can be reduced to the Holling-II but not to the ratio-dependent functional response.

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1. Introduction

The well-known Holling (1959) type II functional response

\[ F_1(x) = \frac{ax}{1+ahx}, \]  

(1.1)

which gives the average number of prey consumed by one predator per unit of time when the prey density is \( x \), is usually derived using a time-budgeting argument. Indeed, (1.1) is based on the assumption that predators divide their time into searching (hunting) for prey and handling (i.e., killing, eating and digesting) the prey caught. The parameters \( a \) and \( h \) have clear-cut and important biological interpretations: \( a \) is the rate at which searching predators attack prey and \( h \) is the expected time a predator handles its prey. An easy computation, see Holling (1959), shows that, on average, a predator spends a fraction \( 1/(1+ahx) \) of its time searching. This immediately leads to the functional response (1.1). An alternative derivation, based on separating the short time scale of searching and handling prey from the long time scale of giving birth and dying, can be found in Metz and Diekmann (1986, p. 6–7).

DeAngelis et al. (1975) and independently Beddington (1975) proposed a generalisation of the Holling functional response (1.1), namely

\[ F_2(x,y) = \frac{\mu x}{\alpha x + \beta y + \gamma}. \]  

(1.2)

Since the publication of the papers (Beddington, 1975; DeAngelis et al., 1975), and especially in the past 20 years, predator–prey models with the functional response (1.2) have been studied in detail (Cantrell and Cosner, 2001; Li and Takeuchi, 2011; Zeng and Fan, 2008; Zhang and Chen, 2006). Purely mathematical results include determination of steady states, investigation of their stability, permanence and bifurcation theory.

Proponents of the DeAngelis–Beddington functional response (1.2) emphasise that it generalises both the Holling type II functional response and the ratio-dependent functional response advocated by Arditi and Ginzburg (1989). Indeed, taking \( \beta = 0 \) one arrives at (1.1) and taking \( \gamma = 0 \) one arrives at the ratio-dependent functional response. However, the ratio-dependent functional response has been criticized, e.g., by Abrams (1994, 1997) on sound theoretical and empirical grounds.
The drawback of the functional response (1.2) is that, to our knowledge, it has never been given a biologically convincing mechanistic derivation in which the parameters $\alpha$, $\beta$, $\gamma$, $\mu$ are given biological interpretations in terms of individual behaviour: Beddington’s (1975) original derivation, a time-budgeting argument similar to the one in Holling (1959), is flawed by the oblivious assumption that the encounter rate between individual predators is independent of the number of interactions already going on; but also the alleged derivations in Broome et al. (2010), Cosner et al. (1999), Huisman and de Boer (1997), Ruxton et al. (1992) and Van der Meer and Smallegange (2009), which are based on a time-scale argument, are not mechanistic in a strict sense, because their analyses yield solutions, for which the original DeAngelis–Beddington functional response is only an approximation. Therefore, these derivations do not yield clear-cut biological interpretations of the parameters in terms of individual behaviour.

The purpose of this paper is to give a very simple mechanistic derivation of the DeAngelis–Beddington functional response, very much in the spirit of the derivation of the Holling functional response using a time-scale separation, and which, for the first time, involves prey refuges instead of the usual interference among predators as in Beddington (1975), Broome et al. (2010), Cosner et al. (1999), Huisman and de Boer (1997), Ruxton et al. (1992) and Van der Meer and Smallegange (2009). Surprisingly, in our derivation the term $b/H$ in the denominator of (1.2) reflects the behaviour of the prey and not the predator. In addition, we show that the parameter $\gamma$ is not a parameter at all and should be fixed at 1. Therefore, the ratio-dependent functional response is not a special case of the functional response (1.2), and it has not been given a mechanistic derivation. We doubt that it will ever be given one. Although Cosner et al. (1999) gives a number of mechanistic explanations of the ratio-dependent functional response, they hold only for high predator densities, whereas the dynamics differing from Holling II type models stem from the singularity at the origin of the ratio-dependent functional response.

2. The main result

As in the derivation of the Holling type II functional response (Metz and Diekmann, 1986), we divide the predator population ($y$) into searchers ($S$) and handlers ($H$). As before, the attack rate is denoted by $a$ and the handling time by $h$. But now we also structure the prey population ($x$) into two classes: the class $P$ of active prey (typically foraging) and prone to predation, and the class $R$ of those prey individuals who have found a refuge (or have become practically invulnerable to attack in some other way such as immobility or an increased level of alertness) and cannot be (or are not) caught by predators. It is conceivable that the more predators there are, the more eager the prey individuals are to move to the refuge. One could argue that only searching predators should influence the rate at which prey move to the refuge, but handling predators can still be felt by prey, for instance by olfaction (Apellbach et al., 2005; Peckarsky et al., 2008). We therefore assume that the rate at which $P$-individuals move to the refuge is proportional to the density of predators, that is, equals $by$ for some positive number $b$. Even if it might be true that prey in the refuge can sense the density of predators and therefore may prefer to stay longer in the refuge if the predator density is high, we assume that the sojourn time in the refuge is independent of the density of the predator and has mean $\tau$. With the assumptions mentioned above, we can write the following system of ordinary differential equations for the short time scale:

$$\frac{dS}{dt} = -aSP + \frac{1}{h}H,$$

$$\frac{dP}{dt} = -byP + \frac{1}{\tau}R - aSP,$$

$$\frac{dR}{dt} = byP - \frac{1}{\tau}R,$$

where

$$y = S + H,$$

$$x = P + R.$$}

The term $-aSP$ in (2.3) becomes negligible if we assume that the predator is rare relative to the prey and that $b$ is large in comparison to the other parameters (to avoid that the term $byP$ vanishes as well). Alternatively, but to the same effect, we may assume that $a$ and $h^{-1}$ are small relative to $b$ and $\tau^{-1}$, in which case no assumptions on relative population densities are needed. Thus ignoring the term $-aSP$ in (2.3) and putting the derivatives on the left-hand sides of (2.1)–(2.4) equal to zero and using (2.5) and (2.6), one finds the quasi-steady state numbers (densities) of searching predators and $P$-prey individuals as

$$S = \frac{y}{1 + ahP},$$

and

$$P = \frac{x}{1 + bry},$$

respectively. Recalling that searchers attack prey prone to predation at a per capita rate $a$, we find that the number of prey consumed per unit of time is

$$aPS = \frac{a}{(1 + bry)(1 + ahP)} = \frac{ax}{1 + bry + ahx}y = F_2(x,y),$$

with $F_2(x,y)$ given by (1.2) with parameters $\mu = a$, $\alpha = ah$, $\beta = br$ and $\gamma = 1$.

We have thus derived the DeAngelis–Beddington functional response based on assumptions made on individual behaviour. The derivation is “direct” in the sense that no further approximations are needed to obtain the result. If there is no refuge, that is, if $b=0$ and/or $\tau = 0$, then the functional response $F_2$ reduces to the Holling type II functional response $F_1$. But because the constant term in the denominator is equal to 1 and hence cannot be varied, $F_2(x,y)$ cannot be reduced to a function of merely $y/x$ and so we cannot justify the ratio-dependent functional response in this way.

We conclude by briefly discussing the consequences of relaxing two of the more obvious model assumptions, namely that the average sojourn time in the refuge is independent of the predator density, and that the active prey seeks refuge in response to the overall predator density rather than the density of searching predators. First, it can be seen in the last step in Eq. (2.9) we recover the DeAngelis–Beddington functional response if, and only if the average sojourn time $\tau$ is independent of the predator density. Second, if active prey reacts to the density of searching predators only, then at the quasi equilibrium has a more complicated form involving square roots, which upon substitution into Eq. (2.9) does not yield the DeAngelis–Beddington functional response either. The mechanistic derivation of the functional response thus requires rather specific assumptions. It is important to know these assumptions to understand what the DeAngelis–Beddington functional response implies about the behaviour of the individual prey and predator.
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References