A derivation of Holling's type I, II and III functional responses in predator-prey systems

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Abstract

Predator-prey dynamics is most simply and commonly described by Lotka-Volterra-type ordinary differential equations (ODEs) for continuous population density variables in the limit of large population sizes. One popular extension of these ODEs is the so-called Rosenzweig–MacArthur model in which various interaction rates between the populations have a nonlinear dependence on the prey concentration. Nonlinear 'functional responses' of this type were originally proposed by Holling on the basis of a general argument concerning the allocation of a predator's time between two activities: 'prey searching' and 'prey handling'.

Although these functional responses are constructed in terms of the behaviour of an individual predator, they are routinely incorporated at the population level in models that include reproduction and death. In this paper we derive a novel three variable model for the simplest-possible mathematical formulation of predator-prey dynamics that allows the interplay between these various processes to take place, on their different characteristic timescales. We study its properties in detail and show how it reduces to Holling's functional responses in special limits. As a result we are able to establish direct links between individual-level and population-level behaviour in the context of these well-known functional responses.

1 Introduction

Predator-prey dynamics are an essential tool in mathematical ecology and, specifically, for our understanding of interacting populations in the natural environment [28, 9, 10]. The dynamics of predator-prey interactions is affected by many factors, but even in the simplest possible biologically-relevant form, the dynamics of mathematical models may indicate complex behaviour, for example persistent oscillations of population sizes, or indicate counter-intuitive dependencies on parameters, for example the 'paradox of enrichment' [29] in which an increase in the prey carrying capacity leads either to an increase in the predator population, but not the prey population, at equilibrium, or, catastrophically, such a large increase in predator numbers that the prey population becomes extinct. More recent work, for example by Berryman [8] and Jensen and Ginzburg [21], considers the status of the paradox of enrichment in detail and in particular whether its 'paradoxical' status owes more to theoretical modelling efforts than to reliable experimental results.

The kind of discussion found in [8], [21] and in the recent book [2] provides ample motivation for the careful examination of the foundations on which commonly-used ecological models, usually comprising differential equations, are built. In this paper we present a first principles derivation of the traditional predator-prey dynamical system comprising Lotka-Volterra-like ordinary differential equations (ODEs) for the two population sizes. We do this in a way that incorporates predator behaviour as well as births and deaths, and hence provides a direct derivation of predator-prey dynamics which includes the different 'functional responses' of predators. The term 'functional response' was first used by Solomon [31] but has become particularly associated with the work of Holling [18, 19] through his classification of functional responses into three basic types (denoted types I, II and III); this nomenclature has since been widely adopted in the literature. There are of course contributions by many subsequent authors, including of particular note Rosenzweig and MacArthur [30] and Real [27].

For a comprehensive survey of work on functional responses, with a discussion of many models that include specific additional biological details see Jeschke et al [22]. For a more mathematical approach to population-level differential equations models, see Metz and Diekmann [25]. For a derivation of the functional responses based on spatial scaling laws see [11].

Holling justified the functional forms of types I, II and III using a straightforward argument based on the division of an individual predator's time into two periods: 'searching for' and 'handling of' prey. Time separation arguments in population dynamics, in more mathematical settings, were used in [4] which considered a large, and hierarchically structured population with different time scales (but with deterministic dynamics), and in [3], where the dynamics of a patchy predator-prey model with slow localised growth and fast migration was considered. It was also used implicitly in [27] in a derivation of the type III response based on first order kinetics. In the present paper, we formalise this division of predator activity into two states and show how it leads to Holling's functional forms. Our aim in this paper is to show in detail how a specific probabilistic description of individual behaviour leads to population-level dynamics, described most generally by a partial differential equation (PDE) for the evolution and transport of the probability density for the system state. We consider the simplest possible version of predator-prey dynamics in order to make the derivation as clear as possible. In the general form in which we take the limit of large population sizes, the diffusion terms are small compared to the advection terms: we therefore concentrate on the dynamics of the vector field along which probability density is transported. We show that the advection equation that we derive is well-posed, and that it places the usual mean-field description in a wider context: the deterministic mean-field dynamics are the trajectories of the vector field along which the probability density is transported. We discuss the mean-field model and its relation to Holling's functional response types in detail. The details of the full advection-diffusion PDE model will be discussed elsewhere.

The structure of the paper is as follows. In section 2 we summarise Holling's original argument, so as to set the scene and to enable comparisons and contrasts to be made with the detailed mathematical arguments that follow. In section 3 we describe the stochastic processes that are sufficient to describe predator-prey dynamics, and we compute the leading-order dynamics of the probability distribution. This leads to a new description for the mean-field dynamics in terms of a vector field in $\mathbb{R}^3$. In section 4 we describe how the mean-field ODEs in $\mathbb{R}^3$ may be reduced, in various asymptotic limits, to two-dimensional systems of the traditional kinds proposed by Holling and others. In this way we make explicit links between the microscopic dynamics and the parameters in the ODE models. In section 5 we present a summary of the dynamics of the model and a selection of illustrative numerical results comparing the behaviour in various regimes. Section 6 provides a brief discussion and draws conclusions.

2 Holling's derivation of the predator functional response

In Holling's original papers on predator-prey dynamics [18, 19] the term 'functional response' was introduced primarily to describe the change in the rate of consumption of prey by a predator when the density of prey varied. In simple situations this can be summarised by plotting the number of prey consumed (per unit time) as a function of prey density, see [18, figure 1] and [19, figure 1] for examples. Holling reserved the term 'type I' for the case in which such a plot shows a linear relationship between numbers of prey consumed and prey density, and termed 'type II' the case in which the gradient of the curve decreases monotonically with increasing prey density, eventually saturating at a constant value of prey consumption. 'Type III' behaviour occurs when the gradient of the curve first increases and then decreases with increasing prey density. This 'sigmoidal' behaviour has been attributed (Real, [27]) to the existence of 'learning behaviour' in the predator population. Real in fact lists six distinct behavioural shifts which might move the functional response from type II to type III, for example predators learning more specialised techniques for hunting or prey handling, or learning to focus their search in particular places within the environment.

The type I response is the result of the simple assumption that the probability of a given predator encountering prey in a fixed time interval T_t, within a fixed spatial region, depends linearly on the prey density. Using the notation of Holling's paper [19] we may express this relationship in the form

$$Y = aT_sX, \tag{1}$$

where Y is the number of prey consumed by one predator, X is the prey density, T_s is the time available for searching and a is a constant of proportionality, termed the 'discovery rate' by Holling. In the absence of a need to spend time handling the prey, all the time can be used for searching, i.e. $T_s = T_t$, and we have the type I response: assuming that the predators (having density P) act independently, in a time T_t the total number of prey will be reduced by a quantity aT_tXP. To be precise, the usual formulation of the overall 'type I' response is as a linear relationship for small prey densities, but with a hard cut-off at larger prey densities: in a time T_t the number of prey consumed by one predator is given by $Y = \min\{aT_tX, Y_{\max}\}$, see [18], figure 8.

If in addition each predator requires a handling time b for each individual prey that is consumed, the time available for searching T_s is reduced: $T_s = T_t - bY$. Combining this with (1) leads to $Y = aT_tX - abXY$ which implies

$$Y = \frac{aT_tX}{1 + abX}, \tag{2}$$

which is the 'type II' formulation. In the time interval T_t the total number of prey is therefore reduced by the quantity $aT_tXP/(1 + abX)$. Note that ab is dimensionless and can be interpreted as a ratio of two characteristic times: ab is large if the handling time b is much longer than the typical discovery time $1/a$ and ab is small in the opposite limit; in this case the type II response reduces to the type I case.

The type III response is not so easily formulated just by separating out the handling and searching behaviours. It can be viewed as a generalisation of the type II response (2) to the form

$$Y = \frac{aT_tX^k}{1 + abX^k}. \tag{3}$$

In the literature this has often been motivated by supposing that learning behaviour occurs in the predator population with a consequent increase in the discovery rate as more encounters with prey occur. Since at higher prey densities there will have been more previous encounters, this motivates modifying the discovery rate a so that it increases monotonically with the number of prey: the simplest such modification involves replacing a by aX^{k-1}, for some $k > 1$. The functional form (3) incorporates this modification while preserving the saturation at large prey density X. This sigmoidal functional form is often termed a 'Hill function' in reference to its formulation in the context of chemical kinetics around a century ago, see for example Barcroft and Hill [5] in which such sigmoidal functions are deduced from reaction schemes. Many generalisations of these functional responses have been considered in the literature, and have been proposed on heuristic grounds rather than through systematic derivations [16, 26]. Brauer and Castillo–Chávez [9] discuss additional functional forms, see in particular their Chapter 5.

3 Derivation of the ODEs

Our detailed derivation starts with the stochastic process underlying the dynamics, and our notation follows McKane and Newman [23] and Baxendale and Greenwood [6]. We construct the simplest possible formulation, as far as we are able, in order to keep the analysis clear. We begin by assuming the existence of only one kind of predator and one kind of prey. We consider a collection of N sites, each connected to every other site, i.e. the graph of possible site interactions is the complete graph consisting of N nodes and $N(N-1)/2$ edges. Each site is either occupied by exactly one predator, or occupied by exactly one prey, or is empty. At a time t, we suppose that m of the sites are occupied by prey (prey individuals are denoted $\mathcal{N}$), n are occupied by predators (similarly denoted $\mathcal{P}$), and $N - n - m$ sites are empty (denoted $\mathcal{E}$).

The system evolves stochastically, through a set of processes some of which involve only individual sites and others of which involve pairs of sites. Individual sites evolve according to the rules:

$$\mathcal{P} \overset{d_1}{\to} \mathcal{E}, \qquad \mathcal{N} \overset{d_2}{\to} \mathcal{E},$$

which describe the death of predators and prey, at rates d_1 and d_2 respectively. Pairs of sites evolve stochastically (and independently of other pairs of sites) according to the following rules:

$$\mathcal{N}\,\mathcal{E} \to \mathcal{N}\,\mathcal{N}, \qquad \mathcal{P}\,\mathcal{N} \to \mathcal{P}\,\mathcal{P}, \qquad \mathcal{P}\,\mathcal{N} \to \mathcal{P}\,\mathcal{E},$$

which describe, in turn, birth of new prey filling an empty site, a predator-prey interaction giving rise to the death of the prey and the birth of a new predator, and a predator-prey interaction in which the prey dies but no new predator is born. It is clear that these rules, in particular the predator-prey interaction rules, are implicitly convenient shorthands for a whole range of complex processes including reproduction and maturation of offspring.

In order to take into account Holling's observation of time spent handling prey as well as searching for prey, we introduce minimal additions to the stochastic model described above. Let n_s be the number of predators $\mathcal{P}_\mathrm{s}$ in searching mode and let n_h be the number of predators $\mathcal{P}_\mathrm{h}$ in handling mode (and therefore unable to search for additional prey). The system state is then completely specified by the triple (n_s, n_h, m) and the number of empty sites is given by $N - n_s - n_h - m$. We modify the evolution rules above to yield the rules:

$$
\begin{aligned}
\mathcal{P}_{\mathrm{s}} &\overset{d_1}{\to} \mathcal{E}, && (4)\\
\mathcal{P}_{\mathrm{h}} &\overset{d_1}{\to} \mathcal{E}, && (5)\\
\mathcal{N} &\overset{d_2}{\to} \mathcal{E}, && (6)\\
\mathcal{N}\,\mathcal{E} &\overset{b}{\to} \mathcal{N}\,\mathcal{N}, && (7)\\
\mathcal{P}_{\mathrm{s}}\,\mathcal{N} &\overset{p_1}{\to} \mathcal{P}_{\mathrm{h}}\,\mathcal{P}_{\mathrm{h}}, && (8)\\
\mathcal{P}_{\mathrm{s}}\,\mathcal{N} &\overset{p_2}{\to} \mathcal{P}_{\mathrm{h}}\,\mathcal{E}, && (9)\\
\mathcal{P}_{\mathrm{h}} &\overset{p_3}{\to} \mathcal{P}_{\mathrm{s}}. && (10)
\end{aligned}
$$

As above, the predator-prey interaction terms implicitly combine many complex processes together. It makes sense to consider the handling mode as comprising a much larger class of activities than merely eating: it is more realistic to see 'handling' as the collection of all activities that are not actively searching for prey. This includes reproduction and juvenile maturation as mentioned before, and as indeed must be the case since (8) is the only rule that allows growth in the predator population. In the set of rules given above we are able to separate the transition of predators (when they find prey) from searching to handling mode, from the transition of predators (when they become hungry or mature enough) from handling mode into searching mode: therefore these processes are given independent stochastic rate parameters (p_1 and p_2, and p_3 respectively). More specifically, we can think of the parameters $p_1, \ldots, p_3, b, d_1, d_2$ as per capita transitions rates, i.e., if p stands for any one of these parameters, then $N\Delta tp$ is a probability. In particular, if the problem is rescaled by $1/N$, then p^{-1} can be thought as a characteristic time for the transition to occur.

Although not necessary in the subsequent analysis, it may be useful to interpret (4)–(10) as a birth-death process. In this setting, the transitions (7)–(9) can be regarded as birth events, while (4)–(6) together with (10) can be regarded as death events. Notice also that transition (9) is not necessary; one could omit it and work with an even simpler setting. Nevertheless, it's inclusion allows us to model independently the predation rate and the predator birth rate.

We now turn to the mathematical formulation of this problem as a stochastic process. We fix the number of sites N. Then the system state is defined completely by the triple $\mathbf{n} = (n_s, n_h, m)$ and the stochastic dynamics is that of a discrete Markov Chain. Let $\mathbb{P}(\mathbf{n}, t|\mathbf{n}_0, t_0)$ denote the probability that the system is in state $\mathbf{n}$ at time t given that it was in state $\mathbf{n}_0$ at time t_0, where $t_0 < t$. The Markov property implies the Chapman–Kolmogorov equation

$$
\mathbb{P}(\mathbf{n}, t+s|\mathbf{n}_0, 0) = \sum_{\mathbf{n}'} \mathbb{P}(\mathbf{n}, t+s|\mathbf{n}', t)\mathbb{P}(\mathbf{n}', t|\mathbf{n}_0, 0)
$$

which can be simplified to read

$$
\mathbb{P}(\mathbf{n}, t+s|\mathbf{n}_0, 0) = \sum_{\mathbf{n}'} \mathbb{P}(\mathbf{n}, s|\mathbf{n}', 0)\mathbb{P}(\mathbf{n}', t|\mathbf{n}_0, 0)
$$

since the Markov process here is stationary. Taking $s = \Delta t$ to be a small time increment and suppressing the conditional dependence on the initial condition $\mathbf{n} = \mathbf{n}_0$ at $t = 0$ we write this as

$$
\mathbb{P}(\mathbf{n}, t+\Delta t) = \sum_{\mathbf{n}'} \mathbb{P}_T(\mathbf{n}, \Delta t|\mathbf{n}', 0)\mathbb{P}(\mathbf{n}', t)
$$

which is in the form of an evolution operator generating $\mathbb{P}(\mathbf{n}, t + \Delta t)$ from $\mathbb{P}(\mathbf{n}, t)$.

The conditional probabilities $\mathbb{P}_T$ can be expressed, to leading order in Δt, in terms of transition probabilities $T(\mathbf{n'}|\mathbf{n})$ from the state (n_s, n_h, m) into the state (n'_s, n'_h, m'). For small Δt we expect that at most one of the events (4) - (10) takes place within the time interval $[t, t + \Delta t]$. Taking into account all possible combinations of interacting and non interacting events, and computing the relevant probabilities we obtain the transition probabilities:

$$\begin{aligned}
T(n_s - 1, n_h, m|\mathbf{n}) &= d_1 n_s, \\
T(n_s, n_h - 1, m|\mathbf{n}) &= d_1 n_h, \\
T(n_s, n_h, m - 1|\mathbf{n}) &= d_2 m, \\
T(n_s, n_h, m + 1|\mathbf{n}) &= 2bm\frac{N - n_s - n_h - m}{N - 1}, \\
T(n_s - 1, n_h + 2, m - 1|\mathbf{n}) &= 2p_1 n_s \frac{m}{N - 1}, \\
T(n_s - 1, n_h + 1, m - 1|\mathbf{n}) &= 2p_2 n_s \frac{m}{N - 1}, \\
T(n_s + 1, n_h - 1, m|\mathbf{n}) &= p_3 n_h.
\end{aligned}$$

We further assume that these transitions are independent and take place at constant rates. The probability $\mathbb{P}(\mathbf{n}, t + \Delta t)$ that the system is in state $\mathbf{n}$ at time $t + \Delta t$ can, to leading order in Δt, now be written in terms of $\mathbb{P}(\mathbf{n}, t)$ and the transition probabilities $T(\mathbf{n'}|\mathbf{n})\Delta t$ of transitions between states over the time interval $[t, t + \Delta t]$, as described for example in the textbook by van Kampen [34]. In order to write these transitions in a more compact notation, we introduce the step operators $\mathbb{E}_{n_s}$, $\mathbb{E}_{n_h}$ and $\mathbb{E}_m$ that act to increment the variables indicated by the respective subscripts:

$$\begin{aligned}
\mathbb{E}_{n_s}[f(\mathbf{n})] &:= f(n_s + 1, n_h, m), \\
\mathbb{E}_{n_h}[f(\mathbf{n})] &:= f(n_s, n_h + 1, m), \\
\mathbb{E}_{m}[f(\mathbf{n})] &:= f(n_s, n_h, m + 1).
\end{aligned}$$

The step operators naturally have inverses that decrement the respective arguments by unity. Using the step operators it is straightforward to compute the probability of the system being in the state (n_s, n_h, m) at time $t + \Delta t$:

$$\begin{aligned}
\mathbb{P}(\mathbf{n}, t + \Delta t) = {} & \mathbb{P}(\mathbf{n}, t) + (\mathbb{E}_m^{-1} - 1)[T(n_s, n_h, m + 1|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_m - 1)[T(n_s, n_h, m - 1|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_{n_s}\mathbb{E}_{n_h}^{-1}\mathbb{E}_m - 1)[T(n_s - 1, n_h + 1, m - 1||\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_{n_s} - 1)[T(n_s - 1, n_h, m|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_{n_h} - 1)[T(n_s, n_h - 1, m|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_{n_s}\mathbb{E}_{n_h}^{-2}\mathbb{E}_m - 1)[T(n_s - 1, n_h + 2, m - 1|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] \\
& + (\mathbb{E}_{n_s}^{-1}\mathbb{E}_{n_h} - 1)[T(n_s + 1, n_h - 1, m|\mathbf{n})\Delta t \ \mathbb{P}(\mathbf{n}, t)] + O(\Delta t^2),
\end{aligned} \tag{11}$$

where the transition rates are as given above.

The above explicit calculations describe the dynamics of a population of finite size. We now wish to pass to the ‘thermodynamic limit’ of a population of infinite size. We therefore introduce the scaled real-valued variables $x_s = n_s/N$, $x_h = n_h/N$ and $y = m/N$, jointly written $\mathbf{x} = \mathbf{n}/N$.

Our treatment of the continuum limit departs from van Kampen's formulation at this point since we wish to emphasise the derivation of an advection equation for the continuous probability density in the limit $N \to \infty$, as done for the SIR model in [13]. van Kampen's formulation would, in contrast, focus first on the leading-order mean-field behaviour through the derivation of ODEs for the mean values (ensemble-averaged expectations) denoted $\bar{\mathbf{x}}(t) := \langle \mathbf{n} \rangle / N$. This would proceed, firstly, by multiplying (11) by n_s and summing over all possible system states so that the first term on the right-hand side together with the term on the left-hand side becomes an approximation to $d\langle n_s \rangle/dt$. The assumptions of independence used above are required to replace terms such as $\langle m n_s \rangle$ and $\langle m^2 \rangle$ by $\langle m \rangle \langle n_s \rangle$ and $\langle m \rangle^2$, respectively. Higher-order terms in $1/N$ are ignored. This procedure is then repeated, multiplying (11) by n_h and then by m. Although van Kampen's procedure yields identical equations for the mean-field dynamics and can be systematically extended to consider higher-order terms describing stochastic fluctuations around the mean values, we prefer to continue to work with the entire probability density.

We make three general remarks. Firstly, the advection PDE is exactly equivalent to the ODEs in the case that we have an initial probability density that is a delta function supported on exactly one point. If there is uncertainty in the initial condition then the solution to the PDE describes how the initial probability density distribution is transported through phase space, and hence it describes the current uncertainty of the system at future times. Secondly, depending on the specific stochastic process and scalings, the continuum limit that one obtains may not be an ODE system, but, as in the case of a Moran process, a parabolic PDE, see for example [12]. Finally, while we keep the calculations at a formal level, all the results derived here are rigorous limits. This can be seen either by the classical stochastic methods derived in [15], or by the more recent approaches in [12] using an inverse-numerical analysis procedure, or indeed as set out in [14] through a weak formulation suitable for a discrete-continuous Fokker–Planck equation.

Returning to our preferred method of carrying out the computation, we propose to pass to the continuum limit by defining a probability density in terms of the scaled variables $\mathbf{x}$:

$$P(x_s, x_h, y, t, N) := \frac{\mathbb{P}(N x_s, N x_h, N y, t)}{1/N}. \tag{12}$$

The step operators similarly can be redefined as

$$\mathbb{E}_{x_s}[g(\mathbf{x})] := g(x_s + \tfrac{1}{N}, x_h, y) \equiv \exp\left(\frac{1}{N}\frac{\partial}{\partial x_s}\right) g(\mathbf{x}), \tag{13}$$

$$\mathbb{E}_{x_h}[g(\mathbf{x})] := g(x_s, x_h + \tfrac{1}{N}, y) \equiv \exp\left(\frac{1}{N}\frac{\partial}{\partial x_h}\right) g(\mathbf{x}), \tag{14}$$

$$\mathbb{E}_{y}[g(\mathbf{x})] := g(x_s, x_h, y + \tfrac{1}{N}) \equiv \exp\left(\frac{1}{N}\frac{\partial}{\partial y}\right) g(\mathbf{x}), \tag{15}$$

using the $\exp(\cdot)$ notation as a formal shorthand for a Taylor series expansion up to a sufficiently high order (actually only the first two terms will be needed in what follows). Clearly these expressions are well-defined only for sufficiently smooth functions $g(\mathbf{x})$. The step operators have the obvious inverses and composition properties, for example

$$\mathbb{E}_{x_s}^{-1}[g(\mathbf{x})] := g(x_s - \tfrac{1}{N}, x_h, y) \equiv \exp\left(-\frac{1}{N}\frac{\partial}{\partial x_s}\right) g(\mathbf{x}),$$

and

$$\mathbb{E}_{x_h}\mathbb{E}_{x_s}[g(\mathbf{x})] := g(x_s + \tfrac{1}{N}, x_h + \tfrac{1}{N}, y) \equiv \exp\left(\frac{1}{N}\frac{\partial}{\partial x_h}\right)\exp\left(\frac{1}{N}\frac{\partial}{\partial x_s}\right) g(\mathbf{x}) \equiv \exp\left(\frac{1}{N}\left(\frac{\partial}{\partial x_s} + \frac{\partial}{\partial x_h}\right)\right) g(\mathbf{x}).$$

We now write the evolution of the (discrete) probability density (11) in the form

$$\begin{aligned}
\frac{1}{N\Delta t}\left(P(\mathbf{x},t+\Delta t,N)-P(\mathbf{x},t,N)\right) &= (\mathbb{E}_y^{-1}-1)\left[2by\frac{1-x_s-x_h-y}{1-\frac{1}{N}}P(\mathbf{x},t,N)\right]+(\mathbb{E}_y-1)\left[d_2yP(\mathbf{x},t,N)\right] \\
&+(\mathbb{E}_{x_s}\mathbb{E}_{x_h}^{-1}\mathbb{E}_y-1)\left[2p_2x_s\frac{y}{1-\frac{1}{N}}P(\mathbf{x},t,N)\right]+(\mathbb{E}_{x_s}-1)\left[d_1x_sP(\mathbf{x},t,N)\right] \\
&+(\mathbb{E}_{x_h}-1)\left[d_1x_hP(\mathbf{x},t,N)\right]+(\mathbb{E}_{x_s}\mathbb{E}_{x_h}^{-2}\mathbb{E}_y-1)\left[2p_1x_s\frac{y}{1-\frac{1}{N}}P(\mathbf{x},t,N)\right] \\
&+(\mathbb{E}_{x_s}^{-1}\mathbb{E}_{x_h}-1)\left[p_3x_hP(\mathbf{x},t,N)\right]+O(\Delta t).
\end{aligned}$$

We now follow what is sometimes referred to as the Kramers–Moyal expansion: inserting the series expansions (13) - (15) for the step operators and truncating at $O(1/N^2)$ (for convenience only, we could of course compute higher-order corrections explicitly if desired) we obtain

$$\begin{aligned}
\frac{1}{N\Delta t}\left(P(\mathbf{x},t+\Delta t,N)-P(\mathbf{x},t,N)\right) &= -\frac{1}{N}\frac{\partial}{\partial y}\left(2by[1-x_s-x_h-y]P\right)+\frac{1}{N}\frac{\partial}{\partial y}\left(d_2yP\right) \\
&+\frac{1}{N}\left(\frac{\partial}{\partial x_s}-\frac{\partial}{\partial x_h}+\frac{\partial}{\partial y}\right)\left(2p_2x_syP\right)+\frac{1}{N}\frac{\partial}{\partial x_s}\left(d_1x_sP\right) \\
&+\frac{1}{N}\frac{\partial}{\partial x_h}\left(d_1x_hP\right)+\frac{1}{N}\left(\frac{\partial}{\partial x_s}-2\frac{\partial}{\partial x_h}+\frac{\partial}{\partial y}\right)\left(2p_1x_syP\right) \\
&+\frac{1}{N}\left(-\frac{\partial}{\partial x_s}+\frac{\partial}{\partial x_h}\right)\left(p_3x_eP\right)+O\left(\Delta t,\frac{1}{N^2}\right).
\end{aligned}$$

To pass to the thermodynamic limit we assume that $P(\mathbf{x},t,N)$ has a well-defined limit function $p(\mathbf{x},t)$:

$$p(\mathbf{x},t):=\lim_{N\to\infty}P(\mathbf{x},t,N). \tag{16}$$

In view of the step operators (13) - (15) it is important that the limit function $p(\mathbf{x},t)$ in (16) not only exists but is (sufficiently) smooth so that these series expansions converge.

Passing to the limit $N\to\infty$ we obtain

$$\begin{aligned}
\frac{1}{\Delta t}\left(p(\mathbf{x},t+\Delta t)-p(\mathbf{x},t)\right) &= -\frac{\partial}{\partial y}\left(2by[1-x_s-x_h-y]p\right)+\frac{\partial}{\partial y}\left(d_2yp\right) \\
&+\left(\frac{\partial}{\partial x_s}-\frac{\partial}{\partial x_h}+\frac{\partial}{\partial y}\right)\left(2p_2x_syp\right)+\frac{\partial}{\partial x_s}\left(d_1x_sp\right) \\
&+\frac{\partial}{\partial x_h}\left(d_1x_hp\right)+\left(\frac{\partial}{\partial x_s}-2\frac{\partial}{\partial x_h}+\frac{\partial}{\partial y}\right)\left(2p_1x_syp\right) \\
&+\left(-\frac{\partial}{\partial x_s}+\frac{\partial}{\partial x_h}\right)\left(p_3x_hp\right)+O(\Delta t).
\end{aligned} \tag{17}$$

At leading order in $1/N$, and in the limit $\Delta t\to 0$, we therefore obtain an advection equation

$$\frac{\partial p}{\partial t}+\nabla\cdot(p\mathbf{u})=0, \tag{18}$$

that describes the transport of probability density by the vector field $\mathbf{u}(\mathbf{x})$. Trajectories of $\mathbf{u}(\mathbf{x})$ are given by solving the nonlinear ODEs

$$\begin{aligned} \dot{x}_s &= -2(p_1+p_2)x_s y - d_1 x_s + p_3 x_h, && (19)\\ \dot{x}_h &= 2(p_2+2p_1)x_s y - d_1 x_h - p_3 x_h, && (20)\\ \dot{y} &= 2by(1-x_s-x_h-y) - d_2 y - 2(p_1+p_2)x_s y. && (21) \end{aligned}$$

These three ODEs comprise the usual mean-field description of the dynamics. The above derivation makes clear their relation to the microscopic stochastic description, and the assumptions involved in their derivation. From a thermodynamic viewpoint, the ODE system corresponds to the macroscopic (and therefore observable) state of the system. As observed earlier, the advection PDE retains information as how uncertainty present in the initial conditions evolves in time.

Before proceeding with the analysis, we point out a number of issues: (i) as observed above, if we let $p_2 = 0$, then the dynamics of (19)–(21) are qualitatively unaffected: we will see this later in section 5; (ii) if we set $p_1 = 0$, then the predators will always become extinct – see also Section 5; (iii) if we identify $x = x_s = x_h$, and sum equations (19) and (20), we obtain the so-called Volterra system, as in [23].

Equations (19) - (21) are well-defined within the closed set $S = \{\mathbf{x} \in \mathbb{R}^3 : x_s, x_h, y \geq 0 \text{ and } x_s + x_h + y \leq 1\}$. The set S is flow-invariant since on the intersection of the hyperplane $x_s + x_h + y = 1$ with S we have

$$\frac{d}{dt}(x_s + x_h + y) = -2p_2 x_s y - d_1(x_s + x_h) - d_2 y \leq 0.$$

Theorem 1 in Chalub and Souza [13] can be applied, with only very minor modifications, to show that the advection equation (18) has a unique solution if the initial condition $p(x,0) = p_0(x)$ is supported within an attracting open subset of $\mathbb{R}^3_+$, the orthant of $\mathbb{R}^3$ in which all coordinates are positive.

More precisely, let $U \subset \mathbb{R}^3_+$ be an open set, and let $\mathbf{u} : U \to \mathbb{R}^3$ be a Lipschitz vector field. We say that an open set V with a piecewise smooth boundary, $V \subset U$ is *attracting* for $\mathbf{u}(\mathbf{x})$ if $\phi_t(V) \subseteq V$ for all $t > 0$, where $\phi_t(\mathbf{x}_0) \equiv \mathbf{x}(t)$ is the flow map for the vector field $\mathbf{u}(\mathbf{x})$. Clearly this implies that every point of V has its omega-limit set in V. Let $p_0(\mathbf{x}) \in L^1(V)$ be a smooth, non-negative probability density supported only in V. Then it can be proved that equation (18) subject to the initial condition $p(\mathbf{x},0) = p_0(\mathbf{x})$ has the unique solution given by the method of characteristics:

$$p(\mathbf{x},t) = \mathrm{e}^{Q(\mathbf{x}) - Q(\phi_{-t}(\mathbf{x}))} p_0(\phi_{-t}(\mathbf{x})),$$

where $Q(\mathbf{x})$ is the solution of the ODE $dQ/dt = -\nabla \cdot \mathbf{u}$, i.e.

$$Q(\mathbf{x}(t)) = Q(\mathbf{x}_0) + \int_0^t -\nabla \cdot \mathbf{u}(\mathbf{x}(s))\, ds.$$

Moreover, $p(\mathbf{x},t)$ is non-negative, supported only within V and satisfies

$$\frac{d}{dt}\int_V p(\mathbf{x},t)\, d\mathbf{x} = 0.$$

4 Reductions to planar predator-prey systems

In this section we discuss the dynamics of the mean-field description (19) - (21), making use of possibilities that some transitions might have very different timescales. In what follows we concentrate primarily on the rate parameter p_3 which describes the rate at which predator individuals return to searching mode from handling mode, i.e. $1/p_3$ is the mean length of time spent handling prey. We discuss limits of large and small p_3 in which the system (19) - (21) can be further reduced to a pair of nonlinear ODEs through a slaving argument. Although our computations in this section are are asymptotic rather than rigorous, it would be straightforward, following the methods in Souza [32] if one were so inclined.

4.1 Type I response

If $p_3 \gg 1$ then individuals return quickly to searching mode and the handling time is very short. In this limit we would expect to recover the type-I functional response. If $p_3 \gg 1$ then from (20) it is clear that x_h decays exponentially rapidly until balanced by the nonlinear term. Hence we expect that x_h is essentially slaved to x_s and y. We formalise this by writing $p_3 = \tilde{p}_3/\varepsilon \gg 1$ where $\tilde{p}_3$ is order unity, so that (20) becomes

$$\varepsilon \dot{x}_h \quad = \quad 2\varepsilon(p_2 + 2p_1)x_s y - (\tilde{p}_3 + \varepsilon d_1)x_h,$$

which can be re-arranged to write

$$\begin{aligned} x_h &= \frac{2\varepsilon(p_2 + 2p_1)}{\tilde{p}_3} x_s y - \frac{\varepsilon}{\tilde{p}_3}(d_1 x_h + \dot{x}_h), \\ \Rightarrow x_h &= \frac{2\varepsilon(p_2 + 2p_1)}{\tilde{p}_3} x_s y + O(\varepsilon^2). \end{aligned} \tag{22}$$

Substituting (22) into (19) and (21) yields the 2D predator-prey system

$$\begin{aligned} \dot{x}_s &= 2p_1 x_s y - d_1 x_s + O(\varepsilon), \\ \dot{y} &= (2b - d_2)y\left(1 - \frac{2by}{2b - d_2}\right) - 2(b + p_1 + p_2)x_s y + O(\varepsilon), \end{aligned}$$

which (at leading order in ε) is the usual linear form for the type-I functional response, and agrees, for example, with McKane and Newman [23]. Note that the leading-order equations balance and that the handling stage has been eliminated from the dynamics since it occurs on a timescale that is asymptotically faster than the other processes described by (4) - (9). Thus, intuitively it is clear that the variable x_h plays only an incidental and passive role in the dynamics; the functional response is type I. Additionally, we observe that, since x_h is asymptotically small, we have $x = x_s + O(\varepsilon)$.

4.2 Type II response

In the opposite limit, i.e. when $p_3 \ll 1$, we expect informally that the handling time is long compared to the searching time. From (19), and from informal arguments based on the transition rules, we observe that in this limit x_s decays rapidly until balanced by the other (linear and nonlinear) terms since p_3 controls the number of searching predators and hence x_s should be small. Finding an asymptotic limit in which this idea is expressed asymptotically correctly is not, however quite as straightforward as in section 4.1.

If we let $p_3 = \varepsilon\tilde{p}_3$ be the only rescaling, where $0 < \varepsilon \ll 1$ is a small parameter and $\tilde{p}_3$ is supposed to remain $O(1)$ then, considering the equations to leading order in ε, the system (19) - (21) becomes

$$\begin{aligned} \dot{x}_s &= -2(p_1 + p_2)x_s y - d_1 x_s, \qquad (23) \\ \dot{x}_h &= 2(p_2 + 2p_1)x_s y - d_1 x_h, \\ \dot{y} &= 2by(1 - x_s - x_h - y) - d_2 y - 2(p_1 + p_2)x_s y. \end{aligned}$$

For any (positive) parameter values these equations have only trivial long-time dynamics: (23) indicates that $x_s(t) \to 0$ as $t \to \infty$ since

$$\begin{aligned} \dot{x}_s &= -x_s\left(d_1 + 2(p_1+p_2)y(t)\right) \leq -d_1 x_s, \\ \Rightarrow x_s(t) &\leq x_s(0)\mathrm{e}^{-d_1 t}. \end{aligned}$$

This in turn implies that $x_h(t) \to 0$ as $t \to \infty$ and therefore $y(t) \to (2b - d_2)/(2b)$ as $t \to \infty$, assuming $y(0) > 0$. We conclude that taking only p_3 to be small does not reveal a nontrivial balance that would be necessary to produce useful asymptotic behaviour.

A more useful reduction can be obtained if we consider rescaling time in addition to p_3, letting

$$p_3 = \varepsilon\tilde{p}_3, \qquad \text{and} \qquad \frac{d}{dt} = \varepsilon\frac{d}{d\tau}.$$

From (19) we obtain

$$x_s = \frac{\varepsilon(\tilde{p}_3 x_h - \dot{x}_s)}{2(p_1+p_2)y + d_1} = \frac{\varepsilon\tilde{p}_3 x_h}{2(p_1+p_2)y + d_1} + O(\varepsilon^2), \tag{24}$$

where $\dot{x}_s$ now denotes $dx_s/d\tau$, showing that x_s becomes small, as we anticipated. In particular, we have $x = x_h + O(\varepsilon)$. Substituting (24) into (20) - (21) we find

$$\varepsilon\dot{x}_h = \frac{2(p_2+2p_1)\varepsilon\tilde{p}_3 x_h y}{2(p_1+p_2)y + d_1} - d_1 x_h - \varepsilon\tilde{p}_3 x_h + O(\varepsilon^2), \tag{25}$$

$$\varepsilon\dot{y} = 2by(1 - x_h - y) - d_2 y - \frac{2(p_1+p_2)\varepsilon\tilde{p}_3 x_h y}{2(p_1+p_2)y + d_1} - \frac{2b\varepsilon\tilde{p}_3 x_h y}{2(p_1+p_2)y + d_1} + O(\varepsilon^2). \tag{26}$$

Neither (25) nor (26) is asymptotically balanced, but (26) can be brought into balance by rescaling the coefficients b and d_2 to be small. However there is a difficulty with (25) since we cannot rescale d_1 by an additional factor of ε without changing (24). Biologically, the problem is that predators in handling mode move out of this class in one of two ways: through death (at a rate d_1) or by returning to searching mode (at a rate p_3). If p_3 is small then death is the only leading-order mechanism (and hence $x_h \to 0$) unless it, too, is rescaled to take place on a slower timescale. This can be resolved by taking transitions (4) and (5) to have different rates, say d_{1s} and d_{1h} respectively. A balanced form of (25) can then be obtained by keeping d_{1s} order unity and rescaling $d_{1h} = \varepsilon\tilde{d}_{1h}$. If we rescale $d_{1h} = \varepsilon\tilde{d}_{1h}$ and $(b, d_2) = \varepsilon(\tilde{b}, \tilde{d}_2)$ as well, we obtain the 2D system

$$\dot{x}_h = \frac{2(p_2+2p_1)\tilde{p}_3 x_h y}{2(p_1+p_2)y + d_{1s}} - \left(\tilde{d}_{1h} + \tilde{p}_3\right)x_h + O(\varepsilon), \tag{27}$$

$$\dot{y} = (2\tilde{b} - \tilde{d}_2)y\left(1 - \frac{2\tilde{b}y}{2\tilde{b} - \tilde{d}_2}\right) - x_h y\left(2\tilde{b} + \frac{2(p_1+p_2)\tilde{p}_3}{2(p_1+p_2)y + d_{1s}}\right) + O(\varepsilon), \tag{28}$$

which is both asymptotically balanced and has the characteristic type-II functional response form for the nonlinear terms describing the predator-prey interaction, i.e. a rational nonlinearity of the form $\sim x_h y/(C+y)$ for some constant C. Notice, however, that (28) is not quite in the Holling type-II form due to the term $-2\tilde{b}x_h y$; this is a direct consequence of the demographic competition built in the model. We refer the reader to Section 6 for further discussion of this point.

We remark briefly that keeping a single predator death rate $d_{1s} = d_{1h} = d_1$ but rescaling it so that $d_1 = \varepsilon\tilde{d}_1$, along with the rescalings $p_3 = \varepsilon\tilde{p}_3$ and $\frac{d}{dt} = \varepsilon\frac{d}{d\tau}$, does not give a satisfactory reduced 2D system. Following the same procedure as above, these scalings together yield the following (assuming $y > 0$):

$$x_s = \frac{\varepsilon\tilde{p}_3 x_h}{2(p_1+p_2)y} + O(\varepsilon^2),$$

and hence

$$\varepsilon\dot{x}_h = \frac{(p_2+2p_1)\varepsilon\tilde{p}_3 x_h}{(p_1+p_2)} - \varepsilon x_h(\tilde{d}_1+\tilde{p}_3) + O(\varepsilon^2),$$

which is linear! In this scaling, at leading order the predator population grows without bound if $p_1\tilde{p}_3 > \tilde{d}_1(p_1+p_2)$ or decays to zero if the reverse inequality holds. We remark that it would be entirely equivalent in the above derivation to assume that p_1, p_2, and d_{1s} are asymptotically large compared to p_3, i.e. to write $p_1, p_2, d_{1s} \sim \varepsilon^{-1}$ and then also to rescale $x_s = \varepsilon\tilde{x}_s$.

To summarise, both collections of asymptotic scalings make clear the separation of timescales between the searching process (which naturally includes the death of searching predators) and the handling process. This timescale distinction appears to be crucial in order to derive Holling's type II response. Given the range of activities covered by our definition of the handling activity, one could imagine various plausible biological motivations for an asymptotically large difference between the death rates in searching and handling modes - for example in many cases one could consider the searching process itself to be much more dangerous (to the predator) than the handling activities. The existence (and consequences) of such differences, but without precise quantification, are discussed in [35]. We refer the reader also to [1] for a discussion on how optimal behaviours can shape the functional response and to [20] for some specific examples in insects.

Finally we observe that, as far as the predator-prey transition rates are concerned, the above derivation is valid if either p_1 or p_2 is order one. Nevertheless, we shall see when studying the stability of the equilibria in Section 5 that when both p_1 and p_3 are small the predator population is likely to become extinct.

4.3 Type III response

As discussed in section 2, a type-III functional response describes situations in which the mortality of the prey first increases with prey density at low densities, and then decreases at higher prey densities so that the response curve has a characteristic S-shaped form. In this section we show that a response curve of this form can be generated in a natural way through a modification of our underlying ansatz for individual interactions. We replace the transitions (8) and (9) by interactions involving $k+1$ individuals:

$$\mathcal{P}_{\mathrm{s}}\ \underbrace{\mathcal{N}\,\mathcal{N}\cdots\mathcal{N}}_{k\ \text{times}} \overset{p_1}{\to} \underbrace{\mathcal{P}_{\mathrm{h}}\,\mathcal{P}_{\mathrm{h}}\cdots\mathcal{P}_{\mathrm{h}}}_{k+1\ \text{times}}, \tag{29}$$

$$\mathcal{P}_{\mathrm{s}}\ \underbrace{\mathcal{N}\,\mathcal{N}\cdots\mathcal{N}}_{k\ \text{times}} \overset{p_2}{\to} \mathcal{P}_{\mathrm{h}}\ \underbrace{\mathcal{E}\,\mathcal{E}\cdots\mathcal{E}}_{k\ \text{times}}. \tag{30}$$

These modifications can be seen as a caricature of the 'learning process' idea that lies behind many explanations for biological explanations of type III response. Transitions (29) - (30) capture the idea of a learning process by the lack of any interaction between a predator and fewer than k prey: until a predator sees a sufficiently large number of prey they are not recognised as food (or, at least not consumed). The transition rules (29) - (30) also introduce stronger nonlinearity through enhancing reproduction. More precisely, predators in searching mode, when they encounter k prey, either simply consume them all and switch to handling mode, or reproduce abundantly, producing k offspring which are all initially juvenile and unable to search for prey: they are therefore placed in the handling mode class. We formulate the encounter with k prey individuals as involving $k+1$ sites so that we maintain a description in which each site is in exactly one of four states: sites are occupied by prey, 'searching' predators, 'handling' predators, or are empty.

The adoption of the modified rule (29) - (30) in place of (8) - (9) leads to the modified transition probabilities

$$\begin{aligned}
T(n_s-1, n_h+k+1, m-k|\mathbf{n}) &= p_1(k+1)n_s\frac{m}{N-1}\frac{m-1}{N-2}\cdots\frac{m-(k-1)}{N-k}, \\
T(n_s-1, n_h+1, m-k|\mathbf{n}) &= p_2(k+1)n_s\frac{m}{N-1}\frac{m-1}{N-2}\cdots\frac{m-(k-1)}{N-k}.
\end{aligned}$$

These transition probabilities lead to new terms in equation (17) replacing those with coefficients p_1 and p_2. The probability density now evolves according to a modified version of (17) in which the new terms are

$$\begin{aligned}
\frac{1}{\Delta t}\left(p(\mathbf{x}, t+\Delta t) - p(\mathbf{x}, t)\right) &= \cdots + \left(\frac{\partial}{\partial x_s} - (k+1)\frac{\partial}{\partial x_h} + k\frac{\partial}{\partial y}\right)\left((k+1)x_s y^k p_1 p\right) \\
&\quad + \left(\frac{\partial}{\partial x_s} - \frac{\partial}{\partial x_h} + k\frac{\partial}{\partial y}\right)\left((k+1)x_s y^k p_2 p\right) + O\left(\frac{1}{N}\right).
\end{aligned}$$

After taking the limit $\Delta t \to 0$, and dropping higher-order terms in $1/N$, we obtain the transport equation for probability density. The vector field that corresponds to the mean-field equations now takes the form

$$\begin{aligned}
\dot{x}_s &= -(k+1)(p_1+p_2)x_s y^k - d_1 x_s + p_3 x_h, && (31) \\
\dot{x}_h &= (k+1)(p_2+(k+1)p_1)x_s y^k - d_1 x_h - p_3 x_h, && (32) \\
\dot{y} &= 2by(1-x_s-x_h-y) - d_2 y - k(k+1)(p_1+p_2)x_s y^k, && (33)
\end{aligned}$$

which reduces to (19) - (21) in the case $k=1$. Additionally, we observe that a similar calculation holds if we let $1 \leq k' \leq k$, and replace the transitions (29) and (30) by

$$\begin{aligned}
\mathcal{P}_{\mathrm{s}}\ \underbrace{\mathcal{N}\,\mathcal{N}\cdots\mathcal{N}}_{k\ \text{times}} &\stackrel{p_1}{\to} \mathcal{P}_{\mathrm{h}}\ \underbrace{\mathcal{P}_{\mathrm{h}}\,\mathcal{P}_{\mathrm{h}}\cdots\mathcal{P}_{\mathrm{h}}}_{k'\ \text{times}}\ \underbrace{\mathcal{N}\ \cdots\mathcal{N}}_{k-k'\text{times}}, && (34) \\
\mathcal{P}_{\mathrm{s}}\ \underbrace{\mathcal{N}\,\mathcal{N}\cdots\mathcal{N}}_{k\ \text{times}} &\stackrel{p_2}{\to} \mathcal{P}_{\mathrm{h}}\ \underbrace{\mathcal{E}\,\mathcal{E}\cdots\mathcal{E}}_{k'\ \text{times}}\ \underbrace{\mathcal{N}\ \cdots\mathcal{N}}_{k-k'\text{times}}. && (35)
\end{aligned}$$

In this case, the corresponding mean-field equations are

$$\begin{aligned}
\dot{x}_s &= -(k'+1)(p_1+p_2)x_s y^k - d_1 x_s + p_3 x_h, && (36) \\
\dot{x}_h &= (k'+1)(p_2+(k'+1)p_1)x_s y^k - d_1 x_h - p_3 x_h, && (37) \\
\dot{y} &= 2by(1-x_s-x_h-y) - d_2 y - k'(k'+1)(p_1+p_2)x_s y^k, && (38)
\end{aligned}$$

As in section 4.2 we can now reduce this three-variable mean field description to a 2D system that contains a nonlinear functional response of a form very similar to that usually described as a 'Holling type III' response. We write $p_3 = \varepsilon\tilde{p}_3$ and rescale time: $d/dt = \varepsilon d/d\tau$. Substituting these scalings into (31) we obtain

$$x_s = \frac{\varepsilon(\tilde{p}_3 x_h - \dot{x}_s)}{(k+1)(p_1+p_2)y^k + d_1} = \frac{\varepsilon\tilde{p}_3 x_h}{(k+1)(p_1+p_2)y^k + d_1} + O(\varepsilon^2), \tag{39}$$

where, as before, $\dot{x}_s$ denotes $dx_s/d\tau$, Substituting (39) into (32) - (33) we obtain

$$\varepsilon \dot{x}_h = \frac{(k+1)(p_2+(k+1)p_1)\varepsilon\tilde{p}_3 x_h y^k}{(k+1)(p_1+p_2)y^k+d_1} - d_1 x_h - \varepsilon\tilde{p}_3 x_h + O(\varepsilon^2), \tag{40}$$

$$\varepsilon \dot{y} = 2by(1-x_h-y) - d_2 y - \frac{k(k+1)(p_1+p_2)\varepsilon\tilde{p}_3 x_h y^k}{(k+1)(p_1+p_2)y^k+d_1} - \frac{2b\varepsilon\tilde{p}_3 x_h y}{(k+1)(p_1+p_2)y^k+d_1} + O(\varepsilon^2). \tag{41}$$

As in section 4.2 we distinguish the predator death rates in the searching and handling modes so that d_1 becomes d_{1s} in (31) and d_{1h} in (32); we also introduce additional rescalings in order to balance terms in the limit $0 < \varepsilon \ll 1$: $(d_{1h}, b, d_2) = \varepsilon(\tilde{d}_{1h}, \tilde{b}, \tilde{d}_2)$. We obtain the asymptotically balanced 2D predator-prey system

$$\dot{x}_h = \frac{(k+1)(p_2+(k+1)p_1)\tilde{p}_3 x_h y^k}{(k+1)(p_1+p_2)y^k+d_{1s}} - (d_{1h}+\tilde{p}_3)\, x_h + O(\varepsilon), \tag{42}$$

$$\dot{y} = (2\tilde{b}-\tilde{d}_2)y\left(1-\frac{2\tilde{b}y}{2\tilde{b}-\tilde{d}_2}\right) - 2\tilde{b}x_h y - \frac{k(k+1)(p_1+p_2)\tilde{p}_3 x_h y^k}{(k+1)(p_1+p_2)y^k+d_{1s}} + O(\varepsilon), \tag{43}$$

which coincides with that obtained in section 4.2, equations (27) - (28), in the case $k = 1$. As we observed in Section 4.2 we point out that, due to the term $-2\tilde{b}x_h y$, (43) is slightly different from the standard Holling type-III form. The existence of this term can be traced back to the demographic competition included in the model; see Section 6 for further remarks.

5 Dynamics of the ODEs and numerical examples

In this section we present a stability analysis for the systems (19) - (21) and (31) - (33) together with some numerical examples. The analysis shows that the overall behaviour of these systems is closely related to the MacArthur–Rosenzweig system, in the sense that when the extinction and prey only equilibria are linearly stable they are also globally asymptotically stable equilibria. When the equilibrium corresponding to coexistence of predators and prey exists, it can be either linearly stable or unstable. In the former case, numerical simulations suggest that it is globally stable, whereas in the latter case an attracting periodic orbit emerges. Additionally, the numerical examples presented illustrate the effectiveness of the approximations of full mean-field systems by the asymptotic planar ones discussed in the previous section.

5.1 Stability analysis of (19) - (21)

We first discuss the stability behaviour for the full mean-field systems previously derived. After performing a convenient reparametrisation, we identify two parameter combinations that control the linear stability and, as it turns out, the global stability.

5.1.1 Reparametrisation

In order to study the dynamical properties of (19) - (21), we rescale time by a factor of $(2b)^{-1}$: $t \mapsto \tilde{t}/(2b)$, and write

$$c = \frac{p_1+p_2}{b}, \quad d_s = \frac{d_{1s}}{2b}, \quad d_h = \frac{d_{1h}}{2b}, \quad p = \frac{p_3}{2b}, \quad q = \frac{p_1}{b}$$

Notice that we always have $c > q$. Also we write

$$y_p^* = 1 - \frac{d_2}{2b}.$$

We can then write (19) - (21) in the tidier form

$$\dot{x}_s = -cx_s y - d_s x_s + p x_h, \tag{44}$$

$$\dot{x}_h = (c+q)x_s y - (d_h + p)x_h, \tag{45}$$

$$\dot{y} = y(y_p^* - y) - (c+1)x_s y - x_h y, \tag{46}$$

where we note that, in order to keep full generality, we allow the death rates for x_s and x_h, d_s and d_h respectively, to differ as in section 4.2.

In this parameterisation the asymptotic regimes corresponding to the planar systems can be derived as follows. For type I we take p to be asymptotically large (the handling process is fast), while for type II we take c, q and d_s to be asymptotically large (the whole searching process happens fast).

5.1.2 Equilibria

The reparametrised ODEs (44) - (46) have at most three biologically-relevant equilibrium points (i.e. ones that have all components non-negative) which we denote $\mathbf{x}^e$, $\mathbf{x}^p$ and $\mathbf{x}^c$. These correspond to complete extinction, survival of only the prey, and mutual coexistence, respectively. We write $\mathbf{x} = (x_s, x_h, y)$ and define the parameter combinations

$$y_c^* = \frac{d_s(d_h + p)}{pq - cd_h} \quad \text{and} \quad \eta = \frac{(c+1)(d_h+p)}{(c+q)y_c^*},$$

so that the equilibria are given explicitly as:

$$\mathbf{x}^e = (0,0,0), \qquad \mathbf{x}^p = \left(0,0,y_p^*\right),$$

and

$$\mathbf{x}^c = (x_s^*, x_h^*, y_c^*), \tag{47}$$

where

$$x_h^* = (1+\eta)^{-1}(y_p^* - y_c^*) \quad \text{and} \quad x_s^* = (1+\eta)^{-1}\frac{d_h + p}{(c+q)y_c^*}(y_p^* - y_c^*). \tag{48}$$

Recall that the dynamics are defined on the closed subset $S = \{\mathbf{x} \in \mathbb{R}^3 : x_s, x_h, y \geq 0 \text{ and } x_s + x_h + y \leq 1\}$ of $\mathbb{R}^3$. Clearly we always have $\mathbf{x}^e \in S$. Note also that $y_p^* \in (-\infty, 1)$ and $y_c^* \in \mathbb{R} - \{0\}$. Therefore, we have that $\mathbf{x}^p \in S$ when $y_p^* > 0$, and that $\mathbf{x}^c \in S$, when both $y_c^* > 0$ and $y_p^* > y_c^*$. Moreover, for a given set of parameter values, we necessarily must have only one of the following holding: (a) only $\mathbf{x}^e \in S$; (b) both $\mathbf{x}^e, \mathbf{x}^p \in S$, but $\mathbf{x}^c \notin S$; (c) $\mathbf{x}^e, \mathbf{x}^p, \mathbf{x}^c \in S$. As we shall see below, these three cases also characterise to a great extent the possible dynamics of the system. This information can be summarised as follows, where LS means linearly stable, LU means linearly unstable and GAS means globally asymptotically stable:

In the following subsection we set out the calculations that support the comclusions in the table.

	(a)	(b)	(c)
$\mathbf{x}^e$	GAS	LU	LU
$\mathbf{x}^p$	—	GAS	LU
$\mathbf{x}^c$	—	—	LS or LU

5.1.3 Linear stability

The Jacobian of the system (44) - (46) evaluated at $\mathbf{x}^e$ is

$$J_e = \begin{pmatrix} -d_s & p & 0 \\ 0 & -(d_h+p) & 0 \\ 0 & 0 & y_p^* \end{pmatrix}.$$

Hence, $\mathbf{x}^e$ is linearly stable in case (a), and unstable in cases (b) and (c). For the other two equilibria, with $y \neq 0$, the Jacobian can be written as

$$J = \begin{pmatrix} -cy - d_s & p & -cx_s \\ (c+q)y & -(d_h+p) & (c+q)x_s \\ -(c+1)y & -y & -y \end{pmatrix}.$$

When evaluated at $\mathbf{x}^p$, we find that its characteristic polynomial is given by:

$$p(z) = (z + y_p^*)(z^2 + Az + B),$$

where

$$A = cy_p^* + p + d_s + d_h \quad \text{and} \quad B = d_s(d_h+p)\left(1 - \frac{y_p^*}{y_c^*}\right).$$

$p(z)$ will have only negative roots if, and only if, $y_p^* > 0$ and $B > 0$. This, in turn, implies that

$$\frac{y_p^*}{y_c^*} < 1.$$

Therefore, we have that $\mathbf{x}^p$ is linearly stable in case (b) and unstable in case (c). Finally, when we evaluate J at $\mathbf{x}^c$, we find that its characteristic polynomial is given by

$$p(\lambda) = \lambda^3 - T\lambda^2 + M\lambda - D,$$

where

$$\begin{aligned} T &= -[(c+1)y_c^* + p + d_s + d_h], \\ M &= \frac{y_c^*}{d_h+p}\left[x_s^*(q-c^2) + (d_h+p)^2 + p(c+q),\right] \\ D &= -d_s(d_h+p)(y_p^* - y_c^*). \end{aligned} \tag{49}$$

We assume that $0 < y_c^* < y_p^*$. In this case, $T, D < 0$. Let

$$R = \frac{x_s^* y_c^*(q-c^2)T + d_s(d_h+p)^2}{|T| y_c^*\left[(d_h+p)^2 + p(c+q)\right]}.$$

Then we can write

$$TM - D = |T| \frac{y_c^*}{d_h + p} \left[(d_h + p)^2 + p(c+q) \right] \left(-1 + R(y_p^* - y_c^*) \right)$$

Thus the sign of $TM - D$ is determined by the sign of $-1 + R(y_p^* - y_c^*)$. Hence, if $R(y_p^* - y_c^*) < 1$, we have that $\mathbf{x}^c$ is linearly stable, while it is linearly unstable if the reversed inequality holds.

5.1.4 Global stability

We now turn our attention to the global stability of these equilibria. This analysis is not entirely straightforward, since the systems (44) - (46) is neither competitive nor cooperative, and since the standard Lotka–Volterra integral is not a Lyapunov function, except at the origin.

In the case of $\mathbf{x}^e$, consider the following Lyapunov function:

$$V(x_s, x_h, y) = x_s + x_h + y\,.$$

Computing dV/dt along the flow, we find

$$\dot{V} \quad = \quad -(c-q)x_s y - d_s x_s - d_h x_h - y(x_s + x_h) + y(y_p^* - y),$$

which is negative in the interior of S as long as $y_p^* \leq 0$. Thus, $\mathbf{x}^e$ is globally asymptotically stable in case (a).

To study the stability of $\mathbf{x}^p$, we first establish a preliminary result. Let us assume that $y_p^* > 0$, and let δ, satisfying $0 < \delta \leq 1 - y_p^*$ be given. Then, for $y \geq y_p^* + \delta$, we have from (46) that

$$\begin{aligned} \frac{\dot{y}}{y} &= y_p^* - y - (c+1)x_s - x_h && (50) \\ &\leq -\delta - (c+1)x_s - x_h. && (51) \end{aligned}$$

Hence

$$y(t) \leq C \exp\left(-\delta t - \int_0^t \left((c+1)x_s(s) + x_h(s) \right)\, ds \right).$$

Thus there exists a time T_δ after which any solution we will have that $y(t) \leq y_p^* + \delta$. Let

$$S_\delta = S \cap \{(x_s, x_h, y) \,|\, y \leq y_p^* + \delta\}.$$

We therefore conclude that when $y_p^* > 0$ any solution to (44) - (46) will eventually enter S_δ, and that S_δ is (forward) invariant.

Now we show the global asymptotic stability of $\mathbf{x}^p$ in case (b). Let us assume that either $y_c^* < 0$ or that $y_p^* < y_c^*$, and consider the new Lyapunov function

$$U(x_s, x_h, y) = x_s + \frac{p}{d_h + p} x_h.$$

As before, fix a δ satisfying $0 < \delta < 1 - y_p^*$; if $y_c^* > y_p^*$, we further restrict this choice to be such that $0 < \delta < y_c^* - y_p^*$. Then computing the derivative of U along the flow, we obtain

$$\dot{U} = -d_s \left[1 - \frac{y}{y_c^*} \right] x_s. \qquad (52)$$

Therefore, on S_δ, we have $\dot{U} \leq 0$. Moreover, we have $\dot{U} = 0$ if, and only if $x_s = 0$.

Therefore, La Salle's Invariance Principle implies that the limit set of an orbit in the interior of S must be either $\mathbf{x}^e$, $\mathbf{x}^p$ or $I = \{(0,0,y) \,|\, 0 \leq y \leq y_p^*\}$. If a limit set contains $\mathbf{x}^e$, then it must be equal to I. On the other hand, if a set contains $\mathbf{x}^p$ it cannot contain any other point. Hence $\mathbf{x}^p$ is globally asymptotically stable.

If we consider y_p^* as a bifurcation parameter, the above analysis shows that we have total extinction for $y_p^* \leq 0$, and extinction of the predator if $y_p^* \in (0,1)$, with $y_p^*/y_c^* \leq 1$. If this latter condition is not satisfied, then we must be in the case $y_c^* \in (0,1)$, and $y_p^* \in (y_c^*, 1)$. In this case, the important quantity to compute is $\bar{y}_c = y_c^* + 1/R$. Numerical simulations then suggest that we have a globally asymptotically stable coexistence equilibrium if $\bar{y}_c > 1$. Otherwise, such a globally stable equilibrium is found only if $y_p^* \in (y_c^*, \bar{y}_c)$, and we have a globally attracting periodic orbit when $y_p^* \in (\bar{y}_c, 1)$.

5.1.5 Modifications for (31) - (33)

In this case, for a given positive integer k we redefine the parameters c and q to be

$$c = \frac{(k+1)(p_1+p_2)}{2b} \quad \text{and} \quad q = \frac{k(k+1)p_1}{2b},$$

which agree with the previous definition when $k = 1$. Then the reparametrised system (31) - (33) can be written as

$$\begin{aligned} \dot{x}_s &= -cx_sy^k - d_sx_s + px_h, & (53)\\ \dot{x}_h &= (c+q)x_sy^k - (d_h+p)x_h, & (54)\\ \dot{y} &= y(y_p^* - y) - (kc+1)x_sy^k - x_hy, & (55) \end{aligned}$$

As before, we have three equilibria, with $\mathbf{x}^e$ and $\mathbf{x}^p$ being the same as before, and with $\mathbf{x}^c = (\bar{x}_s^*, \bar{x}_h^*, \bar{y}_c^*)$ given by

$$\begin{aligned} \bar{x}_s^* &= (1+\bar{\eta})^{-1}\tfrac{d_h+p}{(c+q)(\bar{y}_c^*)^k}(y_p^* - \bar{y}_c^*),\\ \bar{x}_h^* &= (1+\bar{\eta})^{-1}(y_p^* - \bar{y}_c^*),\\ \bar{y}_c^* &= \left(\tfrac{d_s(d_h+p)}{pq-cd_h}\right)^{1/k},\\ \bar{\eta} &= \tfrac{(kc+1)(d_h+p)}{(c+q)\bar{y}_c^*}, \end{aligned}$$

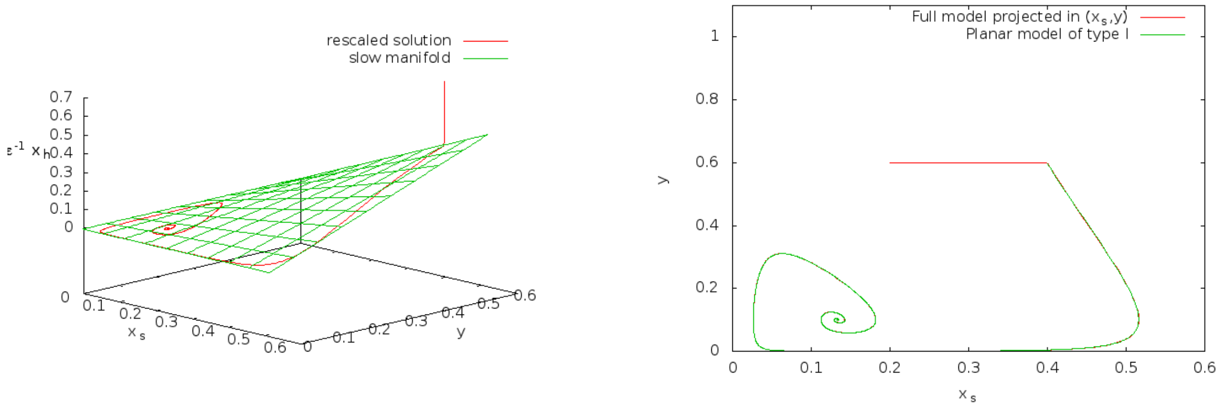
assuming $pq - cd_h > 0$. The linear stability calculations for $\mathbf{x}^e$ are unchanged. For $\mathbf{x}^p$ we now find

$$p(\lambda) = (\lambda + y_p^*)(\lambda^2 + \tilde{A}\lambda + \tilde{B}), \qquad \tilde{A} = c(y_p^*)^k + p + d_s + d_h \quad \text{and} \quad \tilde{B} = d_s(d_h+p)\left(1 - \left(\frac{y_p^*}{y_c^*}\right)^k\right),$$

and hence the same results hold in this case. The nonlinear stability analysis presented in 5.1.4 can be adapted without significant modifications.

5.2 Illustrative numerical results

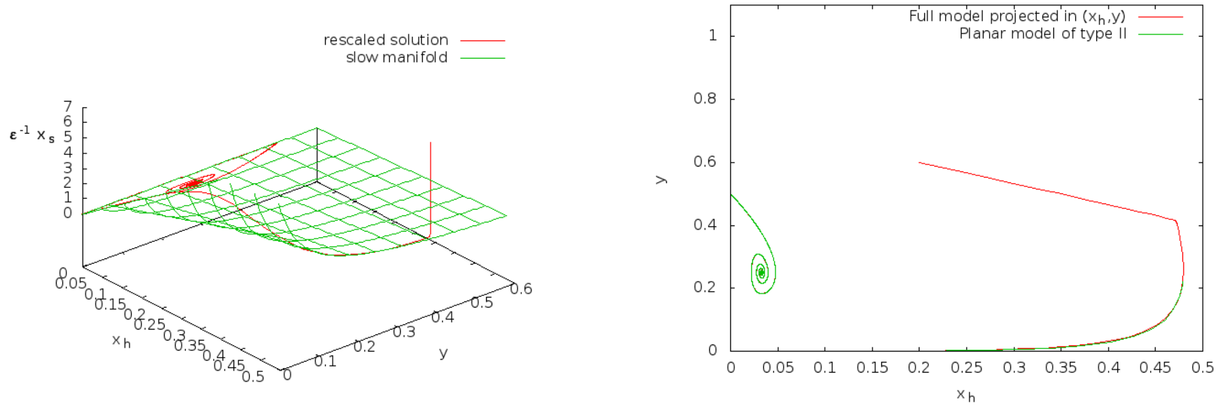
In this section we present numerical simulations that illustrate (i) the accuracy of the asymptotic planar systems derived, and (ii) the dynamical features described above. In the case of small handling times the



(a) (b)

Figure 1: Typical solution trajectories, approaching the mutual coexistence equilibrium $\mathbf{x}^c$, for the full and asymptotically-reduced planar models, in the case of a small handling time. (a) displays a trajectory of the full model. Notice that the number of handling predators diminishes rapidly as suggested by the analysis, until it approaches the 'slaving surface' (slow manifold) for the system. (b) compares the projection of the trajectory in (a) onto the (x_s, y) plane with the trajectory computed from the asymptotically-reduced model for the type-I case. Parameters: $c = 2$, $p = 200$, $q = 1$, $d_s = 0.1$, $d_h = 1$, $y_p = 0.5$. Initial condition: $(x_s, x_h, y) = (0.2, 0.2, 0.6)$.

analysis suggests that we should see a Holling type I behaviour. This is confirmed by the numerical simulations shown in figure 1. In the case of large handling times, the analysis suggests that we should observe Holling type-II behaviour. This case is illustrated in figure 2 (where the coexistence equilibrium is stable) and in figure 3 (where it is unstable and a periodic orbit exists). A similarly close agreement is observed in the case of type III dynamics, comparing the dynamics of (31) - (33) with the reduced system (42) - (43) in the limit of large handling times; this is illustrated, for the case $k = 2$, in figure 4. Figure 5 illustrates a case in which the parameters are not close to one of the asymptotic limits. The periodic oscillation that we observe highlights an additional feature: in cases in which the dynamics is oscillatory all three variables are typically out of phase with each other. As one would expect on biological grounds, a peak in prey numbers leads to a peak in the number of 'handling' predators as the prey are caught; this is followed by a peak in the number of 'searching' predators as the predators move from handling to searching through process (10). Although the system is three-dimensional we have not observed chaotic dynamics for any combinations of parameter values. In this sense, then, we believe (although we have not proved) that the dynamics remains no more complicated than that of planar systems.

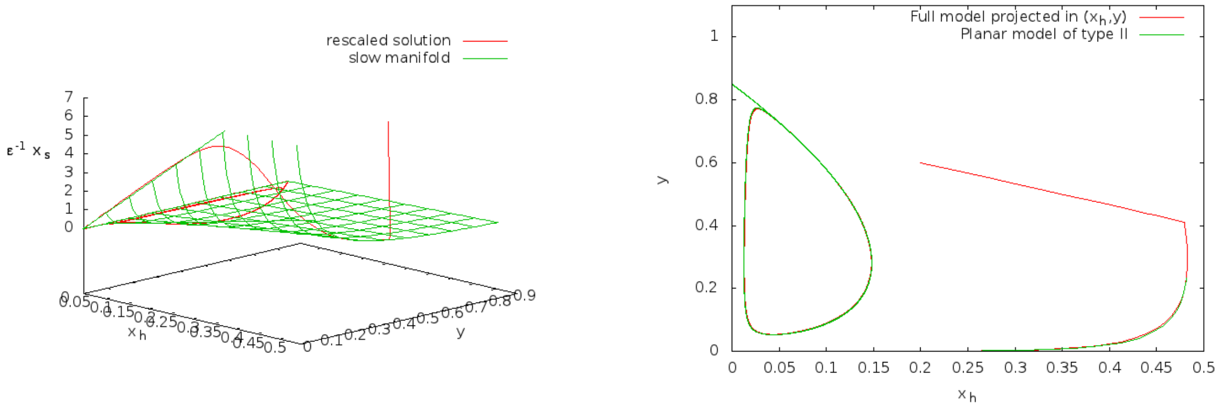


(a) (b)

Figure 2: Typical solution trajectories, approaching the stable mutual coexistence equilibrium $\mathbf{x}^c$, for the full and asymptotically-reduced planar models, in the case of a large handling time. (a) displays a trajectory of the full model. As in figure 1 we note that after an initial transient the trajectory lies close to the slow manifold indicated by the gridded surface. (b) compares the projection of the trajectory in (a) onto the (x_h, y) plane with the trajectory computed from the asymptotically-reduced model for the type-II case. Parameters: $c = 200$, $p = 2$, $q = 100$,$d_s = 10$, $d_h = 0.5$, $y_p = 0.5$. Initial condition: $(x_s, x_h, y) = (0.2, 0.2, 0.6)$.

6 Discussion

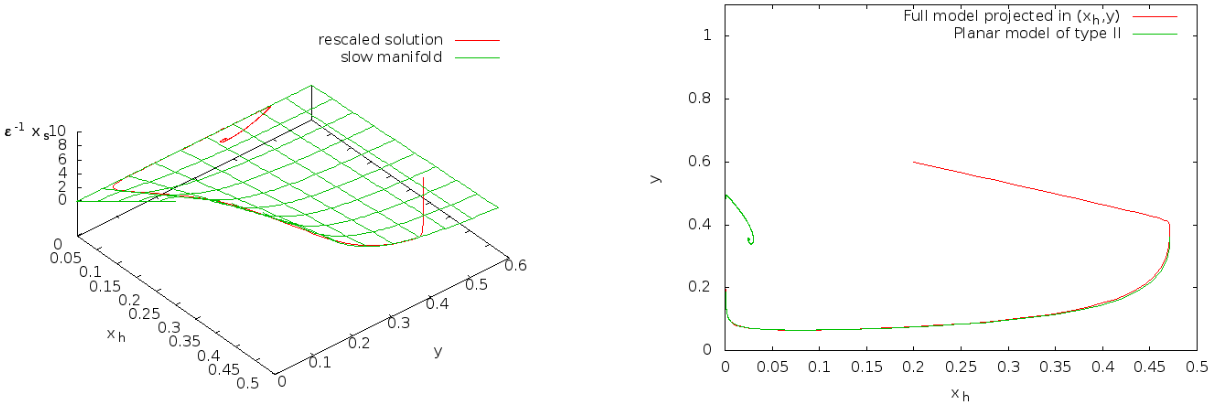
In this paper we have provided a careful first-principles derivation of a system of differential equations describing predator-prey interactions, attempting to derive Holling's type I, II and III classification of predator functional reponses. While Holling's original analyses are not in themselves wrong, they are described in an informal way in which the focus is on the process of predation, separated from the remainder of the lifecycle



(a)

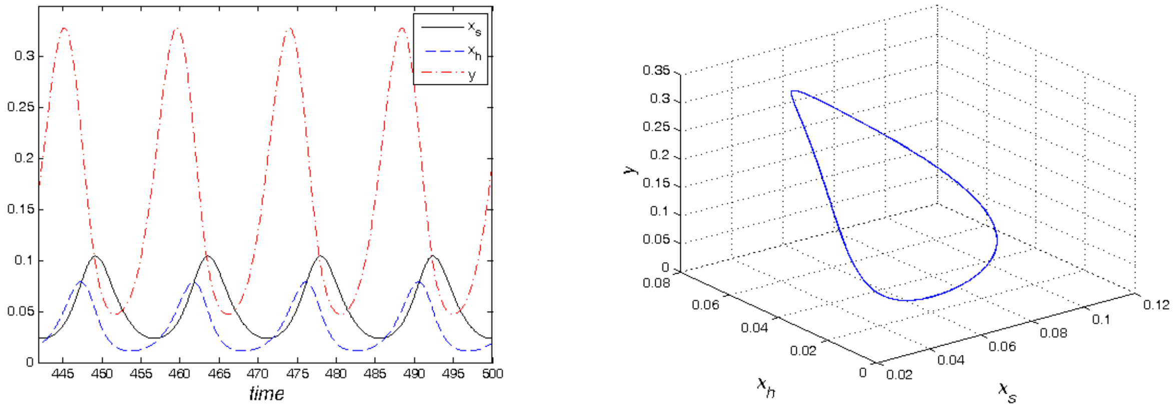
(b)

Figure 3: Typical solution trajectories, approaching a stable periodic orbit in the case that the mutual coexistence equilibrium $\mathbf{x}^c$ is unstable, for the full and asymptotically-reduced planar models, in the case of a large handling time. (a) displays a trajectory of the full model. As in figure 1 we note that after an initial transient the trajectory lies close to the slow manifold indicated by the gridded surface. (b) compares the projection of the trajectory in (a) onto the (x_h, y) plane with the trajectory computed from the asymptotically-reduced model for the type-II case. Parameters: $c = 200$, $p = 1.5$, $q = 100$,$d_s = 7$, $d_h = 0.5$, $y_p = 0.85$. Initial condition: $(x_s, x_h, y) = (0.2, 0.2, 0.6)$.



(a) (b)

Figure 4: Typical solution trajectories, approaching the mutual coexistence equilibrium $\mathbf{x}^c$, for the full and asymptotically-reduced planar models for the case of a nonlinear prey interaction, and in the case of a large handling time. (a) displays a trajectory of the full model (31) - (33). As in figure 1 we note that after an initial transient the trajectory lies close to the slow manifold indicated by the gridded surface. (b) compares the projection of the trajectory in (a) onto the (x_h, y) plane with the trajectory computed from the asymptotically-reduced model (42) - (43) for the type-III case. Parameters take the same values as in figure 2, except that $d_s = 5$ and $k = 2$. Initial condition: $(x_s, x_h, y) = (0.2, 0.2, 0.6)$.



(a) (b)

Figure 5: A stable oscillatory solution for intermediate parameter values. (a) Time plots showing the phase lags between variables. (b) Phase portrait. Parameters: $c = 10$, $p = 3$, $q = 8$, $d_s = 0.5$, $d_h = 1$, $y_p = 0.8$. Initial condition: $(x_s, x_h, y) = (0.2, 0.2, 0.6)$.

of both prey and predator individuals. Our aim in this paper is to embed the distinction between searching and handling behaviour into a complete microscopic description of predator and prey behaviour including birth and death processes, and then to derive, in a self-consistent fashion, a macroscopic population-level collection of differential equations. Such an argument leads naturally to a novel system of three differential equations for the numbers of prey, searching predators and handling predators. These macroscopic equations contain combinations of the various rate coefficients for different microscopic processes, making explicit links between individual and population level behaviour.

In a second stage of the calculation, set out in section 4, in order to recover the Holling type I, II and III functional responses we then consider various asymptotic limits of the timescales associated with different microscopic processes. These limits allow us to eliminate one or other of the variables describing part of the predator population, leaving a 2D system of differential equations for one predator population and the prey. The exact form of the functional responses closely resembles the different types proposed by Holling but, crucially, contains the microscopic rate parameters. This part of the calculation also highlights the way in which these models in general combine processes that for most species occur on a wide range of timescales. It may be that the correct approach in almost every case demands the initial construction of a considerably more complex model, in terms of the number of distinct life stages described for each individual than is currently generally proposed. Then in a second step, careful consideration of the timescales for these different processes allows a reduction in the number of variables; and, starting from the more complex model this can be achieved systematically, with clear and controlled approximations rather than relying purely on biologically-inspired intuition. The full three-variable model describes intermediate regimes between these limits, enabling one to observe the interplay between the two classes of predator; this distinction is not available in the reduced planar models.

A broader point that we intend to make is that, since the macroscopic dynamics can be deduced from microscopic processes, this should be done more frequently when discussing possible modifications to differential equation models for population dynamics. For example, our predator functional responses in (28) and (43) are not quite of the Holling type II and type III forms, respectively due to the $-2\tilde{b}x_h y$ terms. The existence of these terms can be traced back directly to transition rule (7) and the setup of the model to have a fixed number of sites each of which is occupied either by a prey or by a predator. If this constraint is relaxed, for example so that the prey and predator populations occupy distinct collections of sites and do not compete for space, then these terms do not appear.

Of course, many variations on the detailed setup of the microscopic dynamics are possible and we do not claim that we are discussing the most appropriate scheme, biologically speaking, just the simplest construction that illustrates the ideas. For example it would be immediately possible to extend (29) - (30) to allow encounters between a single searching predator and k prey to result in ℓ predators in handling mode and $k-\ell$ empty sites, for $1 \leq \ell \leq k$, instead of just k predators or a single predator. Of the many potential extensions, two that merit careful consideration are, firstly, the inclusion of satiation in the appetite of the predators; see for example [24]. A second potential extension would be to examine the ratio-dependent formulation of the functional response, as discussed recently by Arditi and Ginzburg [2], in which (2) is replaced by the relation

$$Y \quad = \quad \frac{aT_t X/P}{1 + abX/P},$$

where, as before, X and P are the densities of prey and predators, and Y is the number of prey consumed per predator in a time interval T_t.

In conclusion our aim is to inspire the careful construction and use of more complicated models for population dynamics, and for these to be motivated always by consideration of processes at the individual level.

Indeed, the population-level dynamics can then be constructed almost algorithmically from the microscopic data.

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