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Type II functional response for continuous, physiologically structured models

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ABSTRACT

The goal of this work is to formulate a general Holling-type functional, or behavioral, response for continuous physiologically structured populations, where both the predator and the prey have physiological densities and certain rules apply to their interactions. The physiological variable can be, for example, a development stage, weight, age, or a characteristic length. The model leads to a Fredholm integral equation for the functional response, and, when inserted into population balance laws, it produces a coupled system of partial differential–integral equations for the two species, with a nonlocal integral term that arises from rules of interaction in the functional response. The general model is, typically, analytically intractable, but specialization to a structured prey–unstructured predator model leads to some analytic results that reveal interesting and unexpected dynamics caused by the presence of size-dependent handling times in the functional response. In this case, steady-states are shown to exist over long times, similar to the stable age-structure solutions for the McKendick–von Foerster model with exponential growth rates determined by the Euler–Lotka equation. But, for type II responses, there are early transient oscillations in the number of births that bifurcate in a few generations into either the decaying or growing steady-state. The bifurcation parameter is the initial level of prey. This special case is applied to a problem of the biological control of a structured pest population (e.g., aphids) by a predator (e.g., lady beetles).

1. Introduction

There is probably not a more widely known result in population ecology than the Holling type II functional response, or disk equation (Holling, 1959), which measures a predator's per capita feeding rate R (prey per time, per predator) as a function of prey abundance N (prey per area). The response has the form

$$R = \frac{aN}{1 + ahN}, \tag{1}$$

where a is the encounter rate and h is the time it takes a predator to handle a single prey. This follows from the idea that the total time breaks into mutually exclusive times: time to hunt and time to handle. Handling prey itself can be broken into biting, chewing, digesting, etc. (Spalinger and Hobbs, 1992). We do not include this detail in our model, but we do take into consideration that the handling time depends upon both the size of the prey and the size of the predator. Other modifications and extensions include multiple prey, clumped prey (Costner and DeAngelis, 1999), predator interference (Beddington, 1975; DeAngelis et al., 1975; Skalski and Gilliam, 2001), predator–prey ratio dependence and other spatial effects. In a different direction, functional responses may also depend upon environmental variables. For example, daily temperature variations may alter searching times of predators and the activity times of prey, offsetting the interaction opportunities (e.g., Logan et al., 2006; Logan and Wolesensky, 2007a, b), or changes in temperature may put physiological constraints on the predator (Vasseur and McCann, 2005; Wolesensky and Logan, 2007).

In this paper we focus upon the form that the Holling type II response takes in continuous time, age, and physiologically structured predator–prey models. For example, in a size-structured model we must deal with what size of predator consume what size of prey. This is a complex issue and there does not seem to be a general discussion or derivation in the literature; rather, only special cases are studied. In this paper we offer a top-down, comprehensive model of these interactions in the form of a coupled set of reaction–advection partial differential–integral equations for the predator and prey densities (e.g., size densities). The Holling response becomes a nonlocal (integral) term representing a source or sink in the equations. In the general case these equations must be resolved numerically. However, in certain cases the equations can be specialized to simpler systems where analytic progress can be made. We consider one such example where we ask if prey populations can be controlled by the introduction of a uniform predator population, such a case might

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occur in a greenhouse with aphid–lady beetle populations. We point out how other models in the literature arise as a special case of the general equations. The framework we develop leads to many problems with questions of well-posedness that may be of interest to mathematical analysts.

Following the classic works of Lotka, Sharp, and McKendrick in the early 1900s on linear, age-structured models, there have been a large number of papers that address age- and physiologically structured models. General works are, for example, by Metz and Diekmann (1986), Metz et al. (1988), de Roos (1997), Tuljapurkar and Caswell (1997), and Cushing (1998). The latter contains extensive bibliographies on both discrete and continuous models, and it provides an entry point into the literature. Key early papers in this progression are the works by Auslander et al. (1974), who derive a general physiological model and apply it to a host–parasite system, and Gurtin and MacCamy (1974, 1979a, b), who study age-dependent predation. Additional cases where the predator is either indiscriminate or is egg-eating have also been discussed (Gurtin and Levine, 1979; Levine, 1981; Thompson et al., 1982; Coleman and Frauenthal, 1983; Saleem, 1983, 1984). Most authors make simplifying assumptions to make the equations tractable, for example, assuming only one of the trophic populations is structured, or the predator only consumes the eggs of the prey. Some models nicely reduce to systems of ordinary differential equations and the questions of stability can be addressed (e.g., Hastings, 1983). Structured models involving differential-delay equations have been developed by Nisbet (1997); see also the references therein.

The plan of the paper is as follows. To set the stage and notation for the continuous case, in Section 2 we give a brief derivation of the differential equation model for multiple predators consuming discrete sets of prey classes (e.g., size classes). In Section 3 we show how the analysis extends to continuously structured populations of both predators and prey. Of particular note, we formulate and solve a Fredholm integral equation for the functional response. The introduction of the attack rate in the population model leads to a set of coupled partial differential–integral equations for the two population densities. In Sections 4 and 5 we specialize the model to a case where the prey is structured, but the predator population is unstructured. We address the question of determining the threshold value of the prey population for which the prey (a solution to a nonlinear, partial differential–integral equation) either grows exponentially or decays to zero (extinction). Depending upon this parameter, birth rates for the prey oscillate for a few generations before settling to a steady-state. One could equally well consider the initial population of predators as the bifurcation parameter. An application of these ideas gives conditions on the biological control of a pest population.

As a final introductory remark, we explain how we interpret the effects of predation and consumption upon the predator. Typically, for unstructured predators, consumption of prey increases the numbers of individual predators. For structured populations, however, dealing with numbers of individuals does not treat the energetics correctly. Predators in a certain size class do not increase in numbers upon consumption. They may increase their mass, or, indirectly, they may increase their fecundity and add to the number or vitality of new births. Or, for example, increased consumption by some insects may increase their development rates, or their speed through instars. Therefore, one correct way to model structured predators, and prey as well, is to use biomass in place of numbers of individuals. Another interpretation, and the one we take here, is that the payoff for the predator is a decreased mortality rate; that is, consumption of resources reduces natural deaths.

2. Differential equation models

We first review the case where prey of discrete sizes are randomly dispersed in a fixed region of area A. A predator enters the region and encounters prey at a rate depending upon prey size. We follow this with a derivation of the Holling type II response in the case where several predators enter the patch, searching without interference.

2.1. Single predator

Assume a single predator that enters a patch of area A and encounters prey of n different sizes with densities $N_1, \ldots, N_n$. Instead of size, we could equally consider any physiological variable, e.g., development. For easy reference, Table 1 presents various quantities, their definitions, and their dimensions.

For a single predator, the number of attacks on the ith sized prey in time T is

$$r_i = \delta_i S_i T_s N_i, \quad i = 1, 2, \ldots, n, \tag{2}$$

where δ_i, the *detectability*, is the probability of the predator detecting the ith sized prey, S_i is the rate that the predator searches for the ith sized prey, and T_s is the time that the predator spends searching. We define the *encounter rate* of the predator with the ith sized prey by

$$a_i = \delta_i S_i.$$

An important notational choice involves how we denote whether there is an interaction between the predator and the ith sized prey. A separate symbol could be chosen to carry this information; rather, to maintain simple notation, we choose the encounter rate a_i to carry this information. That is, $a_i = 0$ if the predator does not attack the ith sized prey, and $a_i > 0$ if the predator attacks the ith prey.

The total time T available to the predator is the sum of its search time and the total time required to handle all the prey it attacks. The time to handle the jth sized prey is $h_j r_j$, where h_j is the per prey handling time. Therefore,

$$T = T_s + T_h = T_s + \sum_{j=1}^{n} h_j r_j.$$

Substituting into (2), dividing by T, and defining $R_i = r_i/T$ as the predation rate, we have

$$R_i = a_i \left(1 - \sum_{j=1}^{n} h_j R_j \right) N_i. \tag{3}$$

Table 1
Quantities used in the model of an unstructured predator with discretely structured prey.

Quantity	Definition	Dimensions
N_i	Density of ith sized prey	Prey · area^{-1}
S_i	Predator search rate for ith prey	Area · time^{-1} · predator^{-1}
T_s	Predator search time	Time
T_h	Predator's total handling time	Time
T	Predator's total available time	Time
δ_i	Detectability of ith sized prey	Dimensionless
h_i	Predator handling time for ith sized prey	Time · predator · prey^{-1}
R_i	Predation rate on the ith sized prey	Prey · time^{-1} · predator^{-1}
r_i	Number of attacks on ith sized prey	Prey · predator^{-1}
a_i	Encounter rate of the ith sized prey	Area · time^{-1} · predator^{-1}
c_i	Yield from attacks on ith sized prey	Predator · prey^{-1}

Eq. (3) form a system of n linear equations for the predation rates R_i. Writing this system in standard form yields

$$a_iN_i\sum_{j<i}h_jR_j+(1+a_iN_ih_i)R_i+a_iN_i\sum_{j>i}h_jR_j=a_iN_i,\quad i=1,\ldots,n. \tag{4}$$

For $n=3$, for example,

$$\begin{pmatrix}1+a_1N_1h_1 & a_1N_1h_2 & a_1N_1h_3\\ a_2N_2h_1 & 1+a_2N_2h_2 & a_2N_2h_3\\ a_3N_3h_1 & a_3N_3h_2 & 1+a_3N_3h_3\end{pmatrix}\begin{pmatrix}R_1\\R_2\\R_3\end{pmatrix}=\begin{pmatrix}a_1N_1\\a_2N_2\\a_3N_3\end{pmatrix}.$$

It is straightforward to show (e.g., by Cramer's rule) the solution to (4) is given by

$$R_i=\frac{a_iN_i}{1+\sum_{j=1}^n a_jh_jN_j},\quad i=1,\ldots,n. \tag{5}$$

Eqs. (5) define the predation rates of a single predator on n prey classes with densities N_i. These equations represent the *Holling type II response* for n different size classes of prey.

2.2. Multiple-sized predators

For multiple-sized predators we must account for who consumes whom. Suppose, as in the previous subsection, that there are n different prey sizes with densities $N_1,\ldots,N_n$, and there are m different predator types (sizes, development stages, etc.) with populations $P_1,\ldots,P_m$. For example, Fig. 1 depicts the interactions with $n=3$ and $m=2$. The single index i on δ_i, S_i, a_i, h_i, and R_i must now be replaced by a dual set of indices ik (i the prey index and k the predator index). Then, δ_{ik} denotes the detectability of the ith sized prey by the kth sized predator, and $a_{ik}=\delta_{ik}S_{ik}$ is the encounter rate of the ith sized prey by the kth sized predator. The zero encounter rates, e.g., a_{31}, are not indicated in the schematic. Similarly, h_{ik} is the time it takes for the kth sized predator to handle the ith sized prey. It follows immediately from (5) that the per predator attack rate on the ith sized prey is

$$R_{ik}=\frac{a_{ik}N_i}{1+\sum_{j=1}^n a_{jk}h_{jk}N_j},\quad i,k\ \text{fixed}.$$

Therefore, the net attack rate on the ith sized prey by *all* predators is

$$R_i=\sum_{k=1}^m\frac{a_{ik}N_i}{1+\sum_{j=1}^n a_{jk}h_{jk}N_j}.$$

This is the *Holling type II response* for multiple prey and multiple predators. In this case, the population dynamics are given by

$$\frac{dN_i}{dt}=G_i(N_i)-\sum_{k=1}^m\frac{a_{ik}N_i}{1+\sum_{j=1}^n a_{jk}h_{jk}N_j}P_k,\quad i=1,\ldots,n,$$
$$\frac{dP_k}{dt}=-M_k(P_k)+\sum_{i=1}^n\frac{c_{ik}a_{ik}N_i}{1+\sum_{j=1}^n a_{jk}h_{jk}N_j}P_k,\quad k=1,\ldots,m,$$

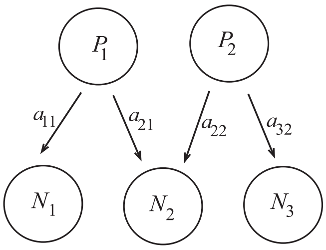

Fig. 1. Diagram showing the predator–prey interactions between two predator classes and three prey size classes. The nonzero a_{ik} denote the encounter rates between the kth sized predator and the ith sized prey.

where c_{ik} are the conversion efficiencies, G_i is the growth rate of prey i, and M_k is the mortality of predator k,

To keep track of the interactions we can store the encounter rates in a matrix $E=(a_{ik})$. For example, the interactions shown in Fig. 1 lead to an encounter matrix of the form

$$E=\begin{pmatrix}a_{11} & 0\\ a_{21} & a_{22}\\ 0 & a_{32}\end{pmatrix}.$$

3. Continuously structured model

Now we develop the general continuous model, starting with the form of the functional response. Then we use the functional response to derive the population equations for the prey and the predator. Key ideas in the model are: handling times for each predator must be integrated over the range of prey sizes that they consume; predation for each prey size must be integrated over a range of predator sizes; and, predation for each predator must be integrated over a range of prey sizes.

3.1. The functional response

Let x and y denote the prey and predator structured variables, respectively, with $0\leqslant x\leqslant X$ and $0\leqslant y\leqslant Y$. The structured variables may represent size, age, mass, development level, or any other structured quantity. Generically, we refer to the variables as size variables. By $u(x,t)$ and $p(y,t)$, in dimensions of individuals per size, per unit area, we denote the densities of the two populations. That is, $u(x,t)\Delta x$ and $p(y,t)\Delta y$ measure the approximate prey and predator populations at time t in the size intervals $[x,x+\Delta x]$ and $[y,y+\Delta y]$, respectively, per unit area. Fig. 2 depicts typical densities. Next, we let the functions $\delta(x,y)$, $S(x,y)$, $h(x,y)$, and $a(x,y)=\delta(x,y)S(x,y)$ denote the detectibility, search speed, handling time, and encounter rate of a predator of size y interacting with prey of size x. As in the discrete case, $a(x,y)=0$ if there is no interaction between prey of size x and predators of size y; thus, $a(x,y)$ carries the interaction information. At time t, for a single predator of size y entering the patch (so, y is fixed), the number of attacks on the prey in size class $[x,x+\Delta x]$ is given by

$$r(x,y,t)\Delta x=\delta(x,y)S(x,y)T_su(x,t)\Delta x=a(x,y)T_su(x,t)\Delta x.$$

The quantity r, an attack density, is measured in prey per size, per predator. The total time T available for the predator's search must be divided into its search time and the time it takes to handle all the prey it attacks; that is, $T_s=T-T_h$. The total handling time is

$$T_h=\int_0^X h(x,y)r(x,y,t)\,dx.$$

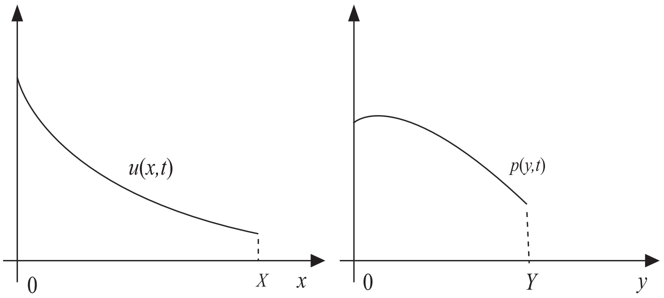

Fig. 2. Typical prey and predator population densities over their size ranges.

Therefore,

$$R(x,y,t)=a(x,y)\left(1-\int_0^X h(x,y)R(x,y,t)\,dx\right)u(x,t), \tag{6}$$

where $R(x,y,t)=r(x,y,t)/T$ is attack rate, measured in prey per size per predator, per unit time. Eq. (6), the continuous analog of the discrete equation (3), is a linear Fredholm integral equation for the attack rate R. We can find its solution using the following device. Define

$$\eta(y,t)=\int_0^X h(x,y)R(x,y,t)\,dx.$$

Then, from (6), R has the form

$$R(x,y,t)=a(x,y)u(x,t)(1-\eta(y,t)). \tag{7}$$

Substituting this back into (6) gives

$$\begin{aligned} &a(x,y)u(x,t)(1-\eta(y,t))\\ &\quad=a(x,y)\left(1-\int_0^X h(x,y)a(x,y)u(x,t)(1-\eta(y,t))\,dx\right)u(x,t).\end{aligned}$$

Because $\eta(y,t)$ is independent of x, it can be brought out of the integral and the last equation can be solved for $\eta(y,t)$, giving

$$\eta(y,t)=\frac{\int_0^X h(x,y)a(x,y)u(x,t),dx}{1+\int_0^X h(x,y)a(x,y)u(x,t)\,dx}.$$

Therefore, from (7), upon simplification, the solution to the integral equation (6) is

$$R(x,y,t)=\frac{a(x,y)u(x,t)}{1+\int_0^X h(x,y)a(x,y)u(x,t)\,dx}. \tag{8}$$

This equation is the continuous analog to (5) and is the Holling type II response for the continuously structured problem. The net predation rate, in prey per time, on the prey in the interval $[x,x+\Delta x]$ is the sum of all the contributions from all the predators, or

$$\text{predation rate}=\Delta x\int_0^Y \frac{a(x,y)u(x,t)}{1+\int_0^X h(\xi,y)a(\xi,y)u(\xi,t)\,d\xi}p(y,t)\,dy,$$

where, for clarity in the sequel, we have changed the dummy variable in the integral in the denominator to ξ.

3.2. *Prey dynamics*

To derive the population law for the prey, we use a *small box method* (see Logan, 2008a) and write a balance equation for the prey in a small range $I=[x,x+\Delta x]$. In words, the time rate of change in the number of prey in I equals the rate that prey enter the region at x, minus the rate that they leave at $x+\Delta x$, minus the rate that they die of natural causes in the interval I, minus the rate that they perish in I by predation. We denote the natural per capita mortality rate by $\mu(x,t)$, and let $g(x,t)$ be the growth rate of prey of size x at time t, or

$$\frac{dx}{dt}=g(x,t). \tag{9}$$

Then the balance law is, symbolically,

$$\begin{aligned}\frac{\partial}{\partial t}(u\Delta x)&=g(x,t)u(x,t)-g(x+\Delta x,t)u(x+\Delta x,t)\\ &\quad-\mu(x,t)u(x,t)\Delta x-\Delta x\int_0^Y R(x,y,t)p(y,t)\,dy.\end{aligned}$$

Dividing by Δx and then taking the limit as $\Delta x\to 0$ gives, after simplification,

$$\begin{aligned}\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(g(x,t)u)&=-\mu(x,t)u\\ &\quad-\int_0^Y\left(\frac{a(x,y)p(y,t)}{1+\int_0^X a(\xi,y)h(\xi,y)u(\xi,t)d\xi}\right)dy.\end{aligned} \tag{10}$$

This nonlinear partial differential–integral equation is the *prey population equation.*

Case 1. Assume that the predator density $p(y,t)$ is given so that we get only a problem for the prey; that is, predators are superimposed upon the system. We assume an initial condition

$$u(x,0)=u_0(x),\quad 0\leqslant x\leqslant X \tag{11}$$

and we impose a McKendrick–von Foerster type boundary condition along $x=0$ of the form

$$g(0,t)u(0,t)=\int_0^X b(x)u(x,t)\,dx, \tag{12}$$

where b is the maternity function (offspring per prey). Then, Eqs. (10)–(12) form a well-posed set of equations for the prey density when the predator density is prescribed. For illustration, we formulate some special cases of the nonlocal term on the right side of (10).

Case 2. As expected, when the handling times are zero, i.e., $h(x,y)=0$, Eq. (10) reduces to the population law with a mass–action (or Lotka–Volterra) type predation term:

$$\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(g(x,t)u)=-\mu(x,t)u-u\int_0^Y a(x,y)p(y,t)\,dy.$$

Case 3. Another simple case, and the one that resembles the classical Holling relationship, occurs when the encounter rate and handling time are constants, i.e., $a(x,y)=a$ and $h(x,y)=h$, and all predators consume all prey. This means the encounter rate and handling rate do not depend on prey or predator sizes. Then (10) becomes

$$\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(g(x,t)u)=-\mu(x,t)u-au\frac{\int_0^Y p(y,t)\,dy}{1+ah\int_0^X u(x,t)\,dx}.$$

The two integrals represent the total populations $U(t)$ and $P(t)$ of the prey and predator, respectively. Thus, the governing population law is simply

$$\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(g(x,t)u)=-\frac{au}{1+ahU(t)}P(t).$$

Case 4. When x is a development variable, given, say, in degree-days, then dx/dt is the rate of development, given in degree-days per day. For many exothermic animals (for example, many arthropods) the development rate is a strongly nonlinear function of temperature, or $r=r(\theta)$. Therefore, if a temperature profile $\theta=\theta(t)$ is prescribed, then

$$\frac{dx}{dt}=r(\theta(t)).$$

Therefore, the growth rate is $g(x,t)=r(\theta(t))$ and the differential operator on the left side of (10) has the form of a simple advection operator $(\partial u/\partial t)+r(\theta(t))(\partial u/\partial x)$. The predation term can also depend upon temperature through the encounter rate. It has been demonstrated in several works (e.g., see Joern et al., 2006, and references contained therein) that the encounter rate can change depending upon temperature-dependent shifts in daily activity times for both the predator and the prey. In this case (10), to which a development dependent natural mortality rate is appended, becomes

$$\frac{\partial u}{\partial t}+r(\theta(t))\frac{\partial u}{\partial x}=-\mu(x,t)u-u\int_0^Y\left\{\frac{a(x,y,\theta(t))p(y,t)}{1+\int_0^X a(\xi,y,\theta(t))h(\xi,y)u(\xi,t)\,d\xi}\right\}dy, \tag{13}$$

which is a generalized, continuously structured version of a nonstructured, discrete model of grasshopper–spider interactions studied by Logan et al. (2006). Upon altering the temperature variation $\theta(t)$ one can use (13) to examine changes in predation level that might be expected under climate changes. Logan (2008b) discusses this type of model when the handling times are zero, or when the functional response is Lotka–Volterra type. See also Logan and Wolesensky (2007a, b).

Finally, we mention an alternate derivation of (8) using the discrete model. If the prey interval $0\leqslant x\leqslant X$ is divided into K equal subintervals of length Δx, then the K prey populations, one for each subinterval, form a discrete set of K different populations, each having individuals of approximately the same size. Then the theory of Section 2 may be applied to obtain discrete attack rates, as in (5). Regarding the sums in these expressions as Riemann sums, and then taking the limit as $\Delta x\to 0$, we obtain the integral form of the response (8). The chief benefit of the derivation above is notational; a discrete-based derivation requires notation with more multiple indices.

3.3. *The predator equation*

Now we derive the balance law for the predator population density. Similar to the prey, discussed above, the balance equation for predators in the arbitrary size interval $[y,y+\Delta y]$ is given by

$$\frac{\partial}{\partial t}[p(y,t)\Delta y]=\gamma(y,t)p(y,t)-\gamma(y+\Delta y,t)p(y+\Delta y,t)-m(y,t)p(y,t)\Delta y+\text{predation rate}, \tag{14}$$

where $dy/dt=\gamma(y,t)$ is the growth rate of predators in the structure variable, and $m(y,t)$ is the per capita mortality rate.

It is important to interpret the predation term accurately. Normally, the predation rate is the net increase in predators in the size interval $[y,y+\Delta y]$ caused by predation on all relevant prey. However, in this case, predation does not increase the number of predators in the $[y,y+\Delta y]$ age class because new predators can enter the population only through birth events. Rather, we may interpret predation as an effect that decreases the mortality of the predators in that class. Simply put, for predators, food availability and predation increase the chance of survival. Another effect of increased predation could be increased predator fecundity during the fertile period, leading to additional offspring. Finally, in some models involving development as the structured variable, increased predation may speed the predator's route through the development period (i.e., increasing $\gamma(y,t)$).

To obtain the form of the predation term we note that $R(x,y,t)\Delta x$ is the rate that prey in the interval $[x,x+\Delta x]$ are consumed by a predator of size y. ($R\Delta x$ is in prey per predator, per unit time). But prey units are converted to predator benefits by $c(x,y)$, the conversion efficiency. Thus $c(x,y)R(x,y,t)\Delta x$ is the rate that prey in $[x,x+\Delta x]$ are converted to a benefit for a predator of size y. Because a predator of size y consumes many sizes of prey, we integrate over all prey to obtain the net benefit. Multiplying by the total number of predators in $[y,y+\Delta y]$, the predation rate is given by

$$\text{predation rate}=p(y,t)\Delta y\int_0^X c(x,y)R(x,y,t)\,dx.$$

Substituting into the balance law (14), dividing by Δy, and then taking the limit as $\Delta y\to 0$, gives the final form of the predator equation:

$$\frac{\partial p}{\partial t}+\frac{\partial}{\partial y}(\gamma(y,t)p)=-m(y,t)p+p\int_0^X\left\{\frac{c(x,y)a(x,y)u(x,t)}{1+\int_0^X a(\xi,y)h(\xi,y)u(\xi,t)\,d\xi}\right\}dx.$$

In summary, the governing equations for the continuous structured predator–prey interaction are

$$\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(gu)=-\mu(x,t)u-u\int_0^Y\left(\frac{a(x,y)p(y,t)\,dy}{1+\int_0^X a(\xi,y)h(\xi,y)u(\xi,t)\,d\xi}\right), \tag{15}$$

$$\frac{\partial p}{\partial t}+\frac{\partial}{\partial y}(\gamma p)=-m(y,t)p+p\int_0^X\left\{\frac{c(x,y)a(x,y)u(x,t)\,dx}{1+\int_0^X a(\xi,y)h(\xi,y)u(\xi,t)\,d\xi}\right\}. \tag{16}$$

To supplement the predator equation, we expect to impose an initial condition

$$p(y,0)=p_0(y),\quad 0\leqslant y\leqslant Y \tag{17}$$

and a birth condition

$$\gamma(0,t)p(0,t)=\int_0^Y\beta(y)p(y,t)\,dy,\quad t>0, \tag{18}$$

where β is the predator's maternity function. Thus, the final form of the model is (15) and (16) along with auxiliary conditions (11), (12), (17), and (18).

Case 5. In the case where the handling time is zero we obtain a generalization of the classical Lotka–Volterra model in the form of a coupled system of nonlocal partial differential equations,

$$\frac{\partial u}{\partial t}+\frac{\partial}{\partial x}(g(x,t)u)=-\mu(x,t)u-u\int_0^Y a(x,y)p(y,t)\,dy,$$
$$\frac{\partial p}{\partial t}+\frac{\partial}{\partial y}(\gamma(y,t)p)=-m(y,t)+p\int_0^X c(x,y)a(x,y)u(x,t)\,dx.$$

This is a generalization of a model studied by Logan (2008a) to examine temperature effects on predation when x and y are development variables (degree-days) and g and γ are development rates (degree-days per day) of the prey and predators, respectively.

Case 6. A model of a different type occurs when the predators only consume the newborns (e.g., the eggs) of the prey. If the structure variable is age, then $g=0$ and the prey equation is

$$\frac{\partial u}{\partial t}+\frac{\partial u}{\partial x}=-\mu(x,t)u.$$

There is no predation term because the PDE holds only on the open interval $0<x<X$. Instead, the predation of newborns affects the initial condition and (12) must be modified. If $P(t)$ denotes the total number of predators at time t, then (12) is replaced by

$$u(0,t)=B(t)-\frac{\alpha B(t)P(t)}{1+\alpha h_e B(t)}, \tag{19}$$

where $B(t)=\int_0^X b(x)u(x,t)\,dx$, α is the encounter rate of a predator with newborns, and h_e is the constant handling time. We require that the right side of (19) is nonnegative; otherwise we take it to be zero. The predator dynamics may be given by a differential equation of the form

$$\frac{dP}{dt}=-mP+\frac{c\alpha B(t)P(t)}{1+\alpha h_e B(t)},$$

where c is the conversion factor. This model is a generalization of that of Saleem (1984).

4. Structured prey with fixed predators

Continuous time, physiologically structured equations like (15) and (16) are analytically intractable and can only be resolved numerically. It is interesting, however, to find special cases that may be solved analytically, either completely or partially. In this section we consider a case where the prey is age-structured and the predator population is fixed. This might be a reasonable model in the case of a generalist predator whose population is largely insensitive to the population of the prey of interest. It might also be reasonable for time periods short enough that the predator population is unaffected by birth and death and predator growth is limited.

We begin with Eq. (10), with some additional simplifying assumptions:

1. The detectability is $\delta = 1$, so that detection is independent of the physiological state.
2. The prey is structured by age, so that $g = 1$.
3. The predator search rate is independent of prey age.
4. The per capita mortality is independent of time.
5. The handling time takes the form $h(x,y) = D(y)w(x)$, where w is the mass of prey of age x and D is the digestion time per unit mass for the predator.

With these assumptions, the prey dynamics can be reformulated as

$$\frac{\partial u}{\partial t} + \frac{\partial}{\partial x}(u) = -\mu(x)u - u\int_0^Y \frac{a(y)p(y)\,dy}{1 + a(y)D(y)\int_0^X w(x)u(x,t)\,dx}. \tag{20}$$

Eq. (20) contains an advection operator, and the right side is a nonlocal source term. To complete the formulation of the problem, we impose an initial condition,

$$u(x,0) = u_0(x), \quad 0 \leqslant x \leqslant X \tag{21}$$

and a boundary condition

$$u(0,t) = B(t) = \int_0^X b(x)u(x,t)\,dx, \quad t > 0, \tag{22}$$

where $b(x)$ is the maternity function (fecundity) for the prey. We make reasonable biological assumptions that h and b are nonnegative, bounded functions with

$$h' > 0, \qquad h(0) = 0, \qquad b(0) = 0.$$

For use in the sequel, we define the cumulative mortality function by

$$M(x) \overset{\text{def}}{=} \int_0^x \mu(s)\,ds. \tag{23}$$

4.1. Asymptotic prey viability

In this model, defined by (20)–(22), we first examine the question of longtime ($t \to \infty$) viability of the prey. Clearly, the partial differential equation shows that the population declines, but the boundary condition boosts the population. The conditions for viability involve the interplay among mortality, predation, and birth.

We first examine the case with *no predation*. Let $v(x,t)$ be the solution to (20)–(22) when $p = 0$. Then we obtain the standard problem

$$\frac{\partial v}{\partial t} + \frac{\partial v}{\partial x} = -\mu(x)v, \quad 0 < x < X, \; t > 0,$$
$$v(x,0) = u_0(x), \quad 0 \leqslant x \leqslant X,$$
$$v(0,t) = B(t) = \int_0^X b(x)v(x,t)\,dx, \quad t > 0.$$

By the method of characteristics (Allen, 2007; Logan, 2008b) the solution to the problem in the region $0 < x < X$, $t > X$ is

$$v(x,t) = B(t-x)e^{-M(x)}.$$

The solution in this region is affected only by the boundary condition, and not the initial condition. It follows that

$$B(t) = \int_0^X b(x)B(t-x)e^{-M(x)}\,dx, \quad t > X.$$

Assume a solution to the form $B(t) = e^{\lambda t}$. Substituting gives an equation for λ,

$$I(\lambda) \overset{\text{def}}{=} \int_0^X b(x)e^{-M(x)-\lambda x}\,dx = 1, \tag{24}$$

which is an analog to the Euler–Lotka equation. We observe that $I(\lambda)$ is continuous and strictly monotone decreasing with $I(\lambda) \to +\infty$ as $\lambda \to -\infty$, $I(\lambda) \to 0$ as $\lambda \to +\infty$. Therefore, there is a unique solution λ^* satisfying $I(\lambda^*) = 1$, and

$$v(x,t) = e^{\lambda^*(t-x)}e^{-M(x)}, \quad 0 < x < t, \; t > X.$$

Consequently, if $\lambda^* < 0$, then $v(x,t) \to 0$ as $t \to \infty$. Finally, because $0 \leqslant u \leqslant v$, we have the result:

$$\text{If } \lambda^* < 0 \quad \text{then} \quad \lim_{t\to\infty} u(x,t) = 0.$$

So, in the case λ^* is negative, the solution to (20)–(22) vanishes as $t \to \infty$.

4.2. Prey control by predation

Next we examine the behavior of models (20)–(22) with $\lambda^* > 0$. We first consider the possibility finding a steady state solution of the form

$$u(x,t) = u_{SS}(x)B(t), \quad u_{SS}(0) = 1, \tag{25}$$

where the steady-state structure u_{SS} and birth rate B are to be determined and $B_0 \overset{\text{def}}{=} B(0)$.

We are specifically looking for population age distributions $u_{SS}(x)$ that are maintained as the population changes and functions $B(t)$ that give the time history of such populations. Later we relax this condition and use a comparison result to obtain the solution behavior for an arbitrary initial population distribution. Substitution of the form (25) into the differential equation (20) yields

$$\left(\frac{B'}{B} + \int_0^Y \frac{a(y)p(y)\,dy}{1 + W_0 a(y)D(y)B}\right)(t) = -\left(\frac{u'_{SS}}{u_{SS}} + \mu\right)(x) = \lambda, \tag{26}$$

where λ is a separation constant to be determined and

$$W_0 \overset{\text{def}}{=} \int_0^X w(x)u_{SS}(x)\,dx. \tag{27}$$

The boundary condition (22) becomes a consistency condition

$$\int_0^X b(x)u_{SS}(x)\,dx = 1. \tag{28}$$

From Eqs. (26) and (28), we obtain the result

$$u_{SS}(x) = e^{-M(x)-\lambda^* x}, \tag{29}$$

where λ^* is again the solution to Eq. (24). The constant W_0 is now determined, and the remaining problem for the birth rate B is

$$B' = (\lambda^* - J[B])B, \quad B(0) = B_0, \tag{30}$$

where B_0 is the given initial birth rate and J is the functional

$$J[B] \overset{\mathrm{def}}{=} \int_0^Y \frac{a(y)p(y)\,dy}{1 + W_0 a(y)D(y)B}. \tag{31}$$

The birth rate equation has a positive equilibrium solution if and only if there exists some $B^* > 0$ for which $J[B^*] = \lambda^*$. Since $J[B^*]$ is monotone decreasing from $J[0]$ to 0 as B increases from 0 to infinity, it follows that there exists a unique positive equilibrium if and only if $J[0] > \lambda^*$; in other words

$$\int_0^Y a(y)p(y)\,dy > \lambda^*. \tag{32}$$

If the predator population does not meet this requirement for a positive equilibrium, then the birth rate (and also the prey population) is monotone increasing. A larger predator population may not control the prey either. The equilibrium birth rate is unstable, so the predator controls the population only if the initial birth rate of the prey population is smaller than the positive equilibrium solution. More simply, we have the following result:

Proposition 1. *Consider problems* (20)–(22) *where* $u_0 = e^{-M(x) - \lambda^* x}$. *If* $J[B_0] > \lambda^*$, *then* $\lim_{t\to\infty} u = 0$. *In particular, the prey population decreases to 0 if the predator population is sufficiently large.*

Now we consider the case that the initial population $u_0(x)$ population is arbitrary. There is always a threshold predator population, given in terms of total search capacity, that is sufficient to control the prey population. We state this formally in the following proposition.

Proposition 2. *Consider problems* (20)–(22) *where* b, w, u_0, μ, a, *and* D *are arbitrary,* M *and* λ^* *are given by* (23) *and* (24), *and*

$$W_0^* \overset{\mathrm{def}}{=} \int_0^X e^{-M(x) - \lambda^* x}\,dx.$$

Then $\lim_{t\to\infty} u = 0$ *whenever*

$$\int_0^Y a(y)p(y)\,dy > \lambda^*[1 + W_0^* D_0 B_0],$$

where

$$D_0 = \max_y [a(y)D(y)], \quad B_0 = \max_x [e^{M(x) + \lambda^* x} u_0(x)].$$

Proof. Let D_0 be the maximum of the function $a(y)D(y)$ and let B_0 be the maximum of the function $e^{M(x)+\lambda^* x} u_0(x)$. Then without loss of generality, suppose that the initial population is increased so that

$$u(x, 0) = B_0 e^{-M(x) - \lambda^* x} \geqslant u_0(x).$$

This change clearly increases both the population and the birth rate for all time; hence, a predator population sufficient to control the increased initial population is certainly sufficient to control the original initial population. Now choose p so that

$$\int_0^Y a(y)p(y)\,dy > \lambda^*[1 + W_0^* D_0 B_0].$$

Then

$$J[B_0] = \int_0^Y \frac{a(y)p(y)\,dy}{1 + W_0^* a(y)D(y)B_0} \geqslant \frac{\int_0^Y a(y)p(y)\,dy}{1 + W_0^* D_0 B_0} > \lambda^*.$$

The prey population, given the increased initial population, decreases to 0 by Proposition 1; hence, so does the prey population with initial population u_0. □

5. Uniform bolus of predators

We now simplify the model further by considering a scenario in which a uniform bolus of P predators is introduced at time 0 into a prey population experiencing unrestricted growth. The initial prey distribution is that of (29), so the total prey population is given by

$$U(t) = CB(t), \quad C = \int_0^X e^{-M(x) - \lambda^* x}\,dx, \tag{33}$$

where problem (30) for B simplifies to

$$B' = B\left(\lambda^* - \frac{aP}{1 + W_0 aDB}\right), \quad B(0) = B_0 = C^{-1}U(0),$$

where a and D are taken to be the values of these functions at the appropriate y corresponding to the bolus of predators. This problem yields the solution in implicit form:

$$t = \frac{1}{aP - \lambda^*}\left(\frac{aP}{\lambda^*}\ln\frac{B - \eta}{B_0 - \eta} - \ln\frac{B}{B_0}\right), \quad \eta = \frac{aP - \lambda^*}{\lambda^* W_0 aD}. \tag{34}$$

Now consider cases with a uniform bolus of predators but with a nonequilibrium initial prey distribution. We must return to the partial differential equation model and apply numerical methods. We assume a bang–bang allocation strategy, in which the prey organisms grow to maturity at age x_D and then begin reproduction. The problem is then given by

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -u\left[\mu + \frac{aP}{1 + aDW(t)}\right], \quad 0 < x < X, t > 0,$$

$$u(0, t) = B(t) = \int_{x_D}^X b(x)u(x, t)\,dx$$

with initial condition (21), where

$$W(t) \overset{\mathrm{def}}{=} \int_0^{x_D} w(x)u(x, t)\,dx + \int_{x_D}^X w_A u(x, t)\,dx, \quad w_A \overset{\mathrm{def}}{=} w(x_D)$$

and with the total prey population given as

$$U(t) = \int_0^X u(x, t)\,dx.$$

For convenience, we nondimensionalize this model, using x_D as the reference time, w_A as the reference for individual weight, $1/x_D$ as the reference for individual birth rate, $1/aD$ as the reference for total population weight, $1/aDw_A$ as the reference for total population, and $1/x_D aDw_A$ as the references for total birth rate and population density u. Thus, we take

$$t = x_D t', \quad x = x_D x', \quad u = \frac{u'}{x_D aDw_A}, \quad w = w_A w', \quad b = \frac{b'}{x_D},$$
$$u_0 = \frac{u_0'}{x_D aDw_A}, \quad U = \frac{U'}{aDw_A}, \quad W = \frac{W'}{aD}, \quad B = \frac{B}{x_D aDw_A}$$

and we define new (dimensionless) parameters by

$$X' = \frac{X}{x_D}, \quad \mu' = x_D \mu, \quad P' = \frac{aP}{\mu}.$$

Thus, X' is the lifetime measured in terms of the development time, $1/\mu'$ is the mean lifespan measured in terms of the development time, and P' is the predator density relative to the minimum predator density necessary for predation to equal natural death in prey population suppression. Given these scales, $W = 1$ is the prey biomass for which the predator functions at half-saturation, $U = 1$ is the population that has unit biomass if exclusively adult, and B is the average adult reproduction during one time unit.

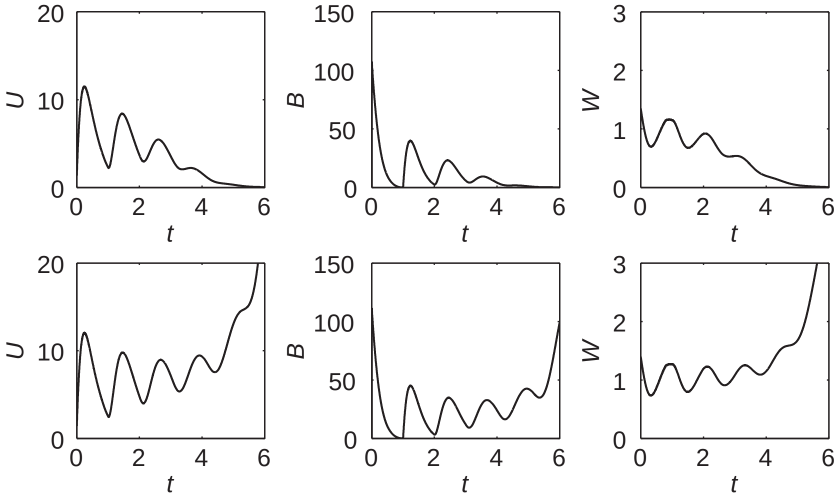

Fig. 3. Numerical solutions to model (35)–(42), with $U_0 = 1.35$ (top row) and $U_0 = 1.4$ (bottom row). Here, U_0 is the initial population level of prey.

After introducing the dimensionless quantities listed above, we obtain the model

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -\mu u\left[1 + \frac{P}{1 + W(t)}\right], \quad 0 < x < X, t > 0, \tag{35}$$

$$W(t) = \int_0^1 w(x)u(x,t)\,dx + \int_1^X u(x,t)\,dx, \tag{36}$$

$$u(0,t) = B(t) = \int_1^X b(x)u(x,t)\,dx, \tag{37}$$

$$u(x,0) = u_0(x), \tag{38}$$

$$U(t) = \int_0^X u(x,t)\,dx. \tag{39}$$

As reasonable examples, we choose the functions

$$w(x) = 8(1 - 2^{-x})^3, \quad b(x) = b_m(X - x). \tag{40}$$

Our choice for w is based on von Bertalanffy growth, with the parameters chosen so that $w(1) = 1$ and the adult length is half the physiological maximum (Ledder et al., 2004). Our choice for b of a linear function with birth rate 0 at $x = X$ is based on data collected for aphids (Tenhumberg et al., 2009). Rather than specifying a value for the parameter b_m, we specify a value for $\lambda^\star$ and then use (24) to calculate b_m, with the result

$$b_m = \frac{(\mu + \lambda^*)^2 e^{\mu + \lambda^*}}{(\mu + \lambda^*)(X - 1) - 1 + e^{-(\mu + \lambda^*)(X - 1)}}. \tag{41}$$

To complete the model specification, we must choose parameters X, μ, $\lambda^\star$, and P, and initial population u_0. For our numerical examples, we choose $X = 2$ and $\mu = 1$, which are reasonable values corresponding to the assumption that the maximum adult survival period, the mean lifespan, and the mean development time are all equal. We choose $\lambda^* = 2$, which corresponds to an assumption that the population doubling time is about one-third of the generation time. Eq. (41) gives us

$$b_m = \frac{9e^3}{2 + e^{-3}} \approx 88.$$

We choose a moderate value $P = 4$, which means that the predator population is sufficient to increase the death rate up to fivefold. For the initial condition, we postulate a population of U_0 individuals with ages uniformly distributed over the interval $[1, 1.2]$, corresponding to an initial prey population consisting of young migrating adults:

$$u_0(x) = 5U_0 H(0.1 - |x - 1.1|), \tag{42}$$

where H is the Heaviside unit step function.

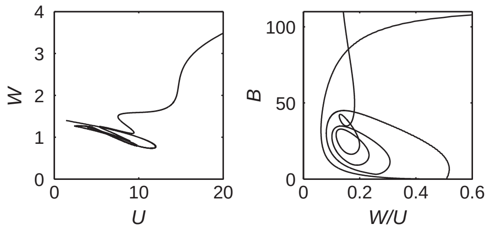

Fig. 4. Phase portraits for model (35)–(42), with $U_0 = 1.4$.

Because the characteristics of (35) are the straight lines $x = t + C$ of speed 1, where C is constant, we can introduce a grid in the xt plane with step sizes Δx and Δt with $\Delta x = \Delta t$. We can then apply a simple upwind method. The integrals are calculated using Simpson's rule and the resulting differential equation integrated with the standard fourth-order Runge–Kutta using MATLAB.

Fig. 3 shows the results of simulations in which the initial prey population is just below and just above the critical value for which the solution bifurcates between prey elimination and prey growth. The graphs show transient oscillations that are due to the large deviation of the initial structure from the steady-state structure (29), with the transition to monotone decay or growth coming after about four generations. The birth rate graph is the most telling. The initial cohort is almost gone by $t = 1$, which is when the next generation is just beginning to mature. Thereafter, there are large oscillations in the birth rate, driven by changes in the population structure. These oscillations are illustrated in Fig. 4 through phase portraits. We see that there is an extended period of oscillation in the mean mass W/U, gradually approaching a value of approximately 0.15. The birth rate follows the trend in the mean mass except for one final oscillation, while the mean mass increases in response to a decrease in the birth rate and vice versa. Eventually, the population approaches its steady structure (29), at which point the ultimate fate of the model is governed by Proposition 2.

6. Summary

We have derived a structured predator–prey model where the interaction is given by a Holling type II functional response. This leads to a set of partial differential–integral equations for the prey and predator densities. The equations are coupled through the nonlinear interaction, or source, terms. It appears that this general model has not been considered in the literature. The examples show that the general equations reduce to several interesting predator–prey models.

The key points in this paper can be summarized as follows:

1. We have derived a top-down, continuous time Holling type 2 response for both physiologically structured predators and prey.
2. Both the handling times and encounter rates can depend upon predator and prey physiological states.
3. Special cases of the model lead to some of the standard structured predator–prey models in the literature.
4. The model provides a toolbox for the study, both practical and theoretical, of a wide array of predator–prey interactions with regard to their age, size, weight, and stage of development. Handling times, or digestion times, can depend upon size, as can discovery rates.
5. Exogenous environmental factors, such as those factors associated with global climate change, can be included in the growth rate functions or the discovery rates. Stochasticity can be included as well.
6. A theoretical and numerical study of a continuously structured prey subject to predation by a unstructured predator whose population is fixed shows an interesting bifurcation and sensitivity with respect to the balance of predator population with the initial prey population and with the structure of the initial prey population. The calculations show oscillations during the first few generations before bifurcating into stable structures that grow or decay, depending upon the initial level of the prey population.
7. The calculations point the way to possible experiments to verify this sensitivity in agriculturally important systems in fields and greenhouses.

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