ORIGINAL ARTICLE

# Phenologically-Structured Predator-Prey Dynamics with Temperature Dependence

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**Abstract** Studies document the fact that temperature changes strongly affect interactions in many consumer-resource systems through altered, or shifted, phenologies. The mistiming of events, such as migration or emergence times, or the contraction or expansion of development times can upset the normal synchronization and lead to increased or decreased predation events. In this paper, we formulate a continuous time, phenologically-structured model of predator-prey interactions that is driven by temperature variations. It is particularly applicable to arthropod interactions because their development rates are so strongly temperature related. The model takes the form of a system of partial differential-integral equations for the species' population densities in development-time variables. In special cases, the model is analytically tractable and we find a closed-form solution. By calculating density variations under different temperature regimes, the model gives a quantitative method for assessing the effects of global temperature change on consumer-resource interactions.

## 1. Introduction

Many experimental studies, too numerous to cite, document the fact that global climate change impacts a variety of species interactions at various trophic levels (for overviews, see Kareiva et al., 1993, Harrington et al., 1999, the bibliography by Burns, 2000, Walther et al., 2002, and especially the review by Visser and Both, 2005). In particular, temperature variations can alter consumer-resource interactions by shifting the species' phenologies (yearly mileposts, such as emergence time, development period, avian migration timing, breeding phenologies, and time of death) and therefore, the temporal association, or timing, of predation events. Spatial associations may be affected as well, and events may also be decoupled by carbon dioxide levels and other environmental factors (Bazzaz, 1990; Hill and Hodkinson, 1992); however, in this communication we only examine temperature effects in the setting of structured, predator-prey dynamics. The key ecological issue

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we address is how changes in synchronization, caused by temperature variations, affect population dynamics.

Even though ecologists have made numerous observations regarding temperature effects on ecosystems, it has been impossible to make long term predictions or carry out field experiments to determine what might occur under extreme environmental conditions. With mathematical models, we are able to simulate different scenarios and make corresponding predictions about the fate of simple, model systems. It is in this spirit, we develop such models. We do not attempt to calculate populations exactly, but rather see how imposed climate variations affect benchmark cases. As eloquently stated by Smith (1974, p. 35), "... it is not necessary that the model be a precise description . . . . What in fact we do is ask what kind of changes in the behavior of the model is made by a particular change in the parameters." The premise of modeling is that comparable changes will occur in the behavior of the biological system. The model we present can be used as a tool for ecologists to input different temperature histories and predict the resulting phenological changes that might occur, including emergence times and species interaction times. This leads to model predictions about the potential changes in populations. How this might proceed in practice will become apparent as the model is developed.

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 on both age- and physiologically-structured equations, linear and nonlinear. General works on structured models of these kinds have been written, for example, by Metz and Diekmann (1986), Metz et al. (1988), de Roos (1997), and Cushing (1998). The latter contains an extensive bibliography on both discrete and continuous models, and it can serve as an entry point to the literature. Here we are interested in continuous time, structured, predator-prey interactions, and so our discussion and citations will focus on this issue. A key, early paper in this progression is the work by Auslander et al. (1974) who derive a general physiological model and apply it to a host-parasite system. Age-dependent predation, where the predator is either indiscriminate or is egg-eating has also been discussed (Gurtin and Levine, 1979; Levine, 1981; Thompson et al., 1982; Coleman and Frauenthal, 1983; Saleem, 1983, 1984, and others). Many 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. Many of these models nicely reduce to systems of ordinary differential equations and the question of stability can be addressed. Otherwise, numerical methods must be used. For example, the recent paper of Garvie (2007) develops a finite-difference scheme for a system of reaction-diffusion equations in space that models a (nonstructured) predator-prey interaction.

Although some prior models include environmental variables, none include temperature variation explicitly, as we do here, and this is the chief contribution of this work. The full, structured, temperature dependent model we develop can only be resolved numerically. To gain tractability, we follow the lead of others and make simplifying assumptions to obtain analytic, close-form solutions. Thus, our goal is to develop a continuous time, physiologically-structured, cohort population model for a consumer and a resource that interact on the basis of their stages of development and their temporal coexistence. In the formulation, we define a general region in joint predator-prey phenology space where the consumer and resource interact; it includes most size-based interactions, including egg-eating predators. The model assumes that there is an underlying temperature history and that the development rates for one or both species, measured in degree-days per day,

are known functions of temperature. Such rates, in fact, have been measured for a large number of exothermic taxa. The final form of the model is a system of reaction-advection partial differential equations for the population densities that is coupled through nonlocal source terms.

A precursor to this work is the recent paper by Logan and Wolesensky (2007b) where a region in a joint phenology space the two species is determined and whose area measures the level of interaction. The region depends on both the possible temporal interaction (timing) and the possible physical interaction of the predator and prey (what sized predator consumes what sized prey). Although this area measure provides a yardstick for the magnitude of an interaction, it does not deal with the issue of population dynamics and the effects of temperature change on population densities. Herein we examine this structured dynamical problem. We opt for a top-down approach where we formulate general equations for interaction and then specialize them to specific cases.

Other works quantitatively address phenological issues with regard to temperature. Wollkind and Logan (1978) have examined McDaniel spider mite-predacious spider mite interactions on apple tree foliage, and Logan and Powell (2001) have modeled the temperature-dependent phenology (oviposition and developmental milestones) of mountain pine beetles to evaluate seasonality in lodgepole pine ecosystems. Also see Bentz et al. (1991), Logan and Bentz (1999), Wermelinger and Seifert (1999), Powell et al. (2000), Rochat and Gutierrez (2001), Gilbert et al. (2004). Specifically relevant to this present work, and providing some of the motivation, the authors and their colleagues (Joern et al., 2005, 2006; Logan et al., 2006, 2007; Wolesensky and Logan, 2007) have experimentally examined and mathematically modeled temperature-dependent wolf spider-grasshopper interactions in grassland ecosystems; and, Logan and Wolesensky (2007a) have investigated predation in a snake-vole system under a stochastic temperature regime. All of these works are discrete-time models and based upon defining a temperature-dependent, predator functional response that modifies the search time for the predator or the daily activity time for the prey.

In summary, this paper develops a continuous time, structured, predator-prey model with Lotka–Volterra (or mass action) type interactions. The model can be extended to one containing other kinds of functional responses, including those that have embedded temperature dependence. The principal contribution is the inclusion of temperature in the model and how temperature variations can affect the phenologies of interacting species and their population dynamics. The form of the model is a new set of coupled differential-integral equations with nonlocal sink and source terms. For reference, Table 1 lists many of the mathematical symbols used in the sequel along with their definitions.

## 2. Temperature, phenology, and interaction

An animal's or plant's development from birth to maturity can be measured by different quantities, for example, a characteristic length, weight, or some other physiological attribute. The speed of development depends upon the species' genetics, nutritional state, and other quantities. In this work, we are interested in poikilothermic species where temperature is the critical factor. Therefore, the development variable commonly used in this case is degree-days. The idea is that a species must accumulate a certain number of days where the temperature is above some minimal threshold level. To be specific, consider an insect like a grasshopper and let $\xi$ denote its development, measured in degree-days, over
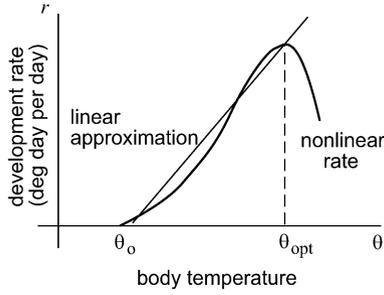
**Fig. 1** Development rate vs. body temperature for a typical terrestrial arthropod. The nonlinear rate function is often approximated by a linear response in a limited temperature range.

its nymphal period from emergence (at hatching or termination of diapause) to maturity; this occurs in many arthropods through a series of stages or instars. We normalize $\xi$ so that $0 \leq \xi \leq 1$, with $\xi = 0$ at emergence and $\xi = 1$ at full development. The time period over which development occurs is the nymphal period $T$. To understand how development evolves over the nymphal period, we denote the *body temperature* of the species by $\theta = \theta(t)$, where $t$ is continuous time measured in days, and body temperature is measured in degrees Celsius. We denote the development rate by $r = r(\theta)$, given in degree-days per day. Figure 1 shows a typical, nonlinear development rate. The development rate $r = r(\theta)$ is frequently taken as a linear function of temperature, giving a $Q_{10}$ type rule (the rate doubles every 10-degree increase in temperature). But, in fact, development rates of most animals are strongly nonlinear functions of temperature, as shown in Fig. 1. There is an optimal temperature $\theta_{\text{opt}}$ where the development rate is maximum, and below a certain threshold temperature $\theta_{\text{min}}$ the development rate is zero. Beyond the optimum temperature there is a rapid fall-off with increasing risk of death. The common, linear response is an approximation for a limited range of temperatures (Fig. 2). Development rates have been measured for many species, both plant and animal, and the data is often fit to a regression curve with specific formula (for example, Hilbert and Logan, 1983, Li and Jackson, 1996 for spiders, Shenk, 1996 for plants, Lactin and Johnson, 1998 for grasshoppers). A theoretical, kinetic basis for such rates is discussed in Gillooly et al. (2002), and the references therein. Thus, the net gain $d\xi$ in degree days over a small time interval period from $t$ to $t + dt$ is approximately $r(\theta(t)) \, dt$. Consequently, by definition,

$$\frac{d\xi}{dt} = r\big(\theta(t)\big), \quad \tau < t < \tau + T, \tag{1}$$

with $\xi(t; \tau) = 0$ at time $t = \tau$, where $\tau$ is the time of emergence. Thus, the parameter $\tau$ is the time a single cohort appears. The nymphal period $T$ depends upon $\tau$, which, for simplicity, is not indicated in the notation; by definition, $\xi(\tau + T; \tau) = 1$, which determines $T$. In principle, there is no restriction on the size of $T$, but from a practical side there is a limit; if $T$ is too long the animals will die because of too slow development. The time of emergence $\tau$ can also shift with temperature change. Further, we assume that both $r$ and $\theta$ are smooth functions of their arguments, and $r \geq 0$. The solution to the differential equation (1) with the given initial condition is a smooth curve

$$\xi = \xi(t; \tau), \quad \tau \leq t \leq \tau + T,$$
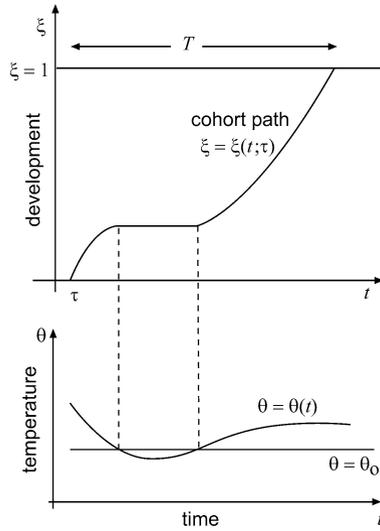
**Fig. 2** Body temperature vs. time and a resulting cohort path. No development occurs when the temperature is below a critical threshold $\theta_0$.

in the $t\xi$ plane. This curve (Fig. 2) represents an individual's (or cohort's) path in physiological space-time ($t\xi$ space), and it can be calculated via direct integration of (1) to get

$$\xi(t;\tau) = \int_\tau^t r\big(\theta(s)\big)\,ds. \tag{2}$$

In the graphical representation in Fig. 2 of physiological space-time we have put $t$ and $\xi$ on the horizontal and vertical axes, respectively; this is opposite a common representation used in applied mathematics (specifically, partial differential equations) where time is on the vertical axis (see Logan 1994, 2006). In the context of advection equations, this path is a characteristic curve. In the present discussion, we refer to it as a *cohort path*, and it is the locus of points in physiological space-time along which development occurs.

As an aside, we may alternately interpret the development interval $0 \le \xi \le 1$ as the development of a single stage or instar. Different instars may have different development rates (for example, see Logan and Powell, 2001).

In summary, if the temperature history and development rate are known, then the species' cumulative development may be calculated by (2). If the cohorts hatch between the times $\tau$ and $\sigma$, with $\sigma > \tau$, then the domain of physiological space-time where the cohorts exist is the region between the two cohort paths $\xi(t;\tau)$ and $\xi(t;\sigma)$ (see Fig. 3). Because different cohorts experience the same temperature at the same time, different cohort paths are shifted vertically from each other when there is a common domain; thus, the speed of the cohort paths along the same vertical line is the same. In special cases the cohort curves can determined analytically.

**Table 1** Table of key symbols and their definitions

| Symbol | Definition |
| --- | --- |
| $t$ | Time |
| $z$ | Generic development coordinate |
| $\xi$ | Normalized prey development variable |
| $\eta$ | Normalized predator development variable |
| $\theta$ | Body temperature |
| $r(\theta), \rho(\theta)$ | Development rates for prey and predator (deg day/day) |
| $u(\xi,t), v(\eta,t)$ | Prey and predator densities |
| $E$ | Physical domain of interaction (size $\eta$ consumes size $\xi$) |
| $\eta_0(\xi)$ | Curve forming the lower boundary of $E$ |
| $J(\xi)$ | The interval $\{\eta : \eta \text{ preys upon } \xi\}$ |
| $I(\eta)$ | The interval $\{\xi : \eta \text{ preys upon } \xi\}$ |
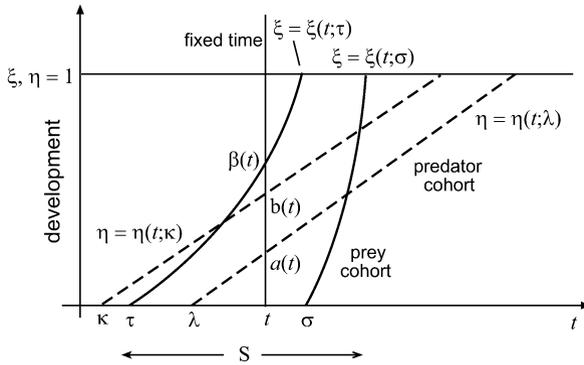


**Fig. 3** Interaction of predator and prey cohorts in development space-time. The prey (solid) and predator (dashed) cohorts emerge in the intervals $\tau \le t \le \sigma$ and $\kappa \le t \le \lambda$, respectively. At a time $t$, prey have nonzero density in $0 \le \xi \le \beta(t)$ and predators have nonzero density in $a(t) \le \eta \le b(t)$. The time interval $S$ is the set of all times that predator and prey coexist.

*Example 1.* A tractable case occurs when the temperature and the development rate are linear functions; that is,

$$r = \alpha\theta - \beta, \quad \theta = \gamma t + \theta_0,$$

where $\beta/\alpha \le \theta \le \theta^*$, where $\theta^*$ is the temperature at maximum development rate, and $\theta_0 \ge \beta/\alpha$. This is the case when the temperature increases linearly during the relevant time period and is in the range where the development rate can be approximated by a linear (e.g., a $Q_{10}$ type rule). Then $r(\theta(t)) = \alpha\gamma t + \alpha\theta_0 - \beta = at + b$, where $a = \alpha\gamma$ and $b = \alpha\theta_0 - \beta$, and the cohort paths (2) in development space-time are family of (concave up) parabolas given by

$$\xi = \frac{a}{2}(t-\tau)^2 + b(t-\tau), \tag{3}$$

where $\tau$ is the time the cohort hatches. The nymphal period $T$ for cohort $\tau$ is determined by solving the quadratic equation $\frac{a}{2}T^2 + bT = 1$, which gives $T = \frac{1}{a}(-b + \sqrt{b^2 + 2a})$.

A similar model can be developed for a predator, or consumer. For the consumer, we assume a development rate $\rho = \rho(\theta)$, and, for simplicity, we assume the predator and prey have the same body temperature.

Before continuing, we remark on a notation convention. Temporarily, it is convenient in the sequel to introduce a different development variable (other than $\xi$) for the predator. This will help clarify the differences in the existence domains of the predator and the prey. We use $\eta$ for predator development. Actually, development for both species occurs in a single, development-time space with coordinates $z$ and $t$, where $z$ is a generic development coordinate between 0 and 1. Therefore, both $\xi$ and $\eta$ are representations of $z$. At the end of the model formulation, we recast the system back into $zt$ variables.

Therefore, for the predator,

$$\frac{d\eta}{dt} = \rho\big(\theta(t)\big),$$

and the predator cohort emerging at time $t = \kappa$ has cohort path

$$\eta = \eta(t; \kappa) = \int_{\kappa}^{t} \rho\big(\theta(s)\big)\, ds,$$

with $\eta(\kappa; \kappa) = 0$ and $\eta(\kappa + T; \kappa) = 1$, where $T$ is the development period (dependent upon $\kappa$). Predator cohorts emerging in the time interval $[\kappa, \lambda]$ will evolve in physiological space-time between the curves $\eta = \eta(t; \kappa)$ and $\eta = \eta(t; \lambda)$, in $0 \leq \xi \leq 1$. Figure 3 shows the development-time interaction between two poikilothermic species; prey emerge in $\tau \leq t \leq \sigma$ and predators emerge in $\kappa \leq t \leq \lambda$.

A key, even though obvious, observation is that both species must be present at the same time for predation to occur. For illustration, at any fixed time $t$, represented by a vertical line in Fig. 3, there is an interval in development space where prey are present ($0 \leq \xi \leq \beta(t)$ in Fig. 3) and an interval where predators are present ($a(t) \leq \eta \leq b(t)$ in Fig. 3). But whether those predators consume the coexisting prey depends upon the physical interaction. Certain sized predators will consume only certain sized prey items. For example, small predators in early stages of development may not consume large prey.
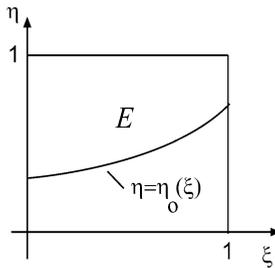


**Fig. 4** The region $E$ in joint development space where development-structured predation occurs, depending upon the development of the predator and prey. The lower boundary of the region is denoted by $\eta = \eta_0(\xi)$. The function $\eta_0$ may also be piecewise defined; for example, if the region $E$ is $0 \leq \xi \leq \frac{1}{2}$, where all predators consume prey of size $\xi \leq \frac{1}{2}$, then $\eta_0(\xi) = 0$ for $\xi \leq \frac{1}{2}$ and $\eta_0(\xi) = 1$ for $\xi > \frac{1}{2}$.

Thus, there is a fixed region $E$ of $\xi\eta$ space defined by the set of $(\xi, \eta)$ for which a predator of size $\eta$ can consume a prey item of size $\xi$. That is,

$$E = \big\{(\xi, \eta) : \text{ predators of size } \eta \text{ consume prey of size } \xi\big\}.$$

See Fig. 4. This size-dependent predation restricts the interactions that take place.

*Remark 1.* As evidenced by the language used above, we are implying a relationship between the size of an animal and its degree of development. We are, however, making no specific assumptions about size structure or what the relationship is, and the term *size* is only used in a descriptive sense.

## 3. Population dynamics

In this section, we formulate a joint-structured population model that governs the phenological densities of the two, interacting populations. The model takes the form of a coupled system of two, nonlinear advection equations. The coupling comes through non-local source terms, which relate to development-dependent predation rates. The prey and predator densities are functions of the development coordinate $z$ and time $t$; but, for clarity, in our derivations we will replace $z$ by $\xi$ for the prey and $\eta$ for the predator; at the end we return to the generic $z$ coordinate to formulate the final equations.

### 3.1. The prey equation

First we set up a prey cohort model. We let $u = u(\xi, t)$ denote the prey population density, i.e., $u(\xi, t) \cdot \Delta\xi$ is the approximate number of prey at time $t$ having development in the interval $[\xi, \xi + \Delta\xi]$. Similarly, $v = v(\eta, t)$ denotes the predator population density, i.e., $v(\eta, t) \cdot \Delta\eta$ is the approximate number of predators at time $t$ having development in the interval $[\eta, \eta + \Delta\eta]$. To formulate the model equations we first visualize generic prey and predator densities at a fixed time $t$. See Figs. 5 and 6.

We obtain the balance law for prey in the standard way, using the *small box* method (see, for example, Logan, 1994, 2006), where the balance is imposed in a small developmental interval. In words, the rate of change of the number of prey in an arbitrarily small development interval $[\xi, \xi + \Delta\xi]$ must equal the net rate that prey enter and leave the interval (prey flux) minus the rate of mortality. Because we are modeling cohorts, there are no births, and we ignore migration. The number of prey in the small development interval $[\xi, \xi + \Delta\xi]$ at time $t$ is approximately

$$u(\xi, t)\Delta\xi.$$

(We prefer this simple approximation characterizing number of prey in the interval rather than to write it as $u(\widetilde{\xi}, t)\Delta\xi$, where $\widetilde{\xi} \in (\xi, \xi + \Delta\xi)$. The distinction disappears since, in the end, we take $\Delta\xi \to 0$. This same remark applies in the sequel as well to the mortality rate and predation rate; we will just evaluate $u$ at $\xi$ and not at some intermediate point in the interval.) The net rate (prey flux) that prey enter and leave the interval $[\xi, \xi + \Delta\xi]$ depends upon the speed of development and is given by

$$\text{flux} = u(\xi, t)r\big(\theta(t)\big) - u(\xi + \Delta\xi, t)r\big(\theta(t)\big).$$
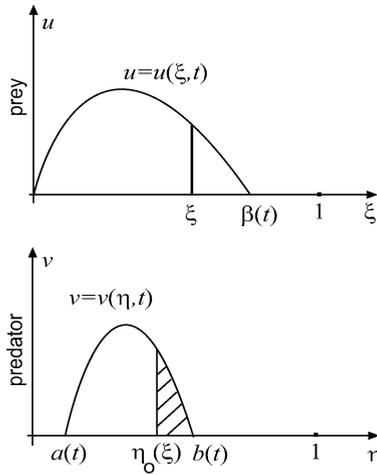
**Fig. 5** Prey and predator densities at a fixed time $t$, consistent with the diagrams in Figs. 3 and 4. The shaded region shows the integrated predator density (shaded) that consumes prey in development stage $\xi$. The intervals $0 \leq \xi \leq \beta(t)$ and $a(t) \leq \eta \leq b(t)$ are defined as in Fig. 3.
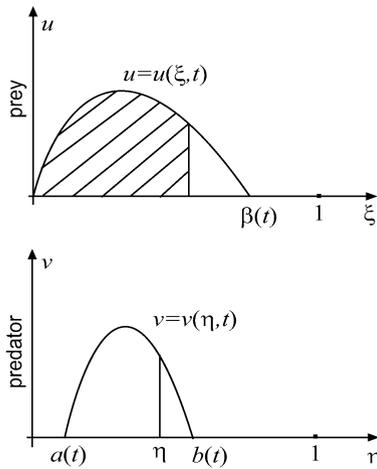


**Fig. 6** Prey and predator densities at a fixed time $t$, showing the prey population (shaded) that is consumed by a predator in development stage $\eta$. The quantities labeled on the plot are consistent with those in Figs. 3 and 4.

Mortality of the prey cohort is of two types, natural mortality and mortality due to predation. We assume the per capita natural mortality rate is given by $m(\xi)$, given in per unit time per prey density, so the total natural mortality rate (prey per time) is approximately

$$m(\xi)u\Delta\xi.$$

To model predation we select the simplest functional response, where the predation rate is proportional to the product of the number of predators and the number of prey (this is Lotka–Volterra kinetics, mass action kinetics, or a Type I response). The number of prey in a small development interval $[\xi, \xi + \Delta\xi]$ is approximately $u(\xi, t)\Delta\xi$, and we denote by $V(\xi, t)$ the total number of predators that consume prey in that interval. Then the predation rate is $kV(\xi, t)u(\xi, t)\Delta\xi$, where $k$ is the rate constant.

We observe that $V$ depends upon predator density, the time of possible interactions, and the sizes of predators that consume the prey. Now, the conservation law for the prey is

$$\frac{\partial}{\partial t}(u\Delta\xi) = u(\xi, t)r\big(\theta(t)\big) - u(\xi + \Delta\xi, t)r\big(\theta(t)\big)$$
$$- m(\xi)u\Delta\xi - kV(\xi, t)u(\xi, t)\Delta\xi.$$

Dividing by $\Delta\xi$ and taking the limit as $\Delta\xi \to 0$ gives the local form of the conservation law for the prey density $u(\xi, t)$:

$$\frac{\partial u}{\partial t} + r\big(\theta(t)\big)\frac{\partial u}{\partial \xi} = -m(\xi)u - kuV(\xi, t).$$
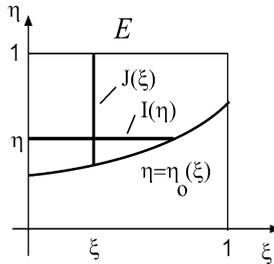
To determine the expression $V$, let

$$J(\xi) = \big\{\eta : (\xi, \eta) \in E\big\}.$$

This is the interval of predator sizes that prey upon the resource of size $\xi$, and it is illustrated in Fig. 7. The total number of predators that interact with prey of size $\xi$ is the integral of the predator density over the interval $J(\xi)$, or

$$V(\xi, t) = \int_{\eta \in J(\xi)} v(\eta, t)\, d\eta.$$

Figure 7 indicates the interval $J(\xi)$. Therefore, the balance law takes the form

$$\frac{\partial u}{\partial t} + r\big(\theta(t)\big)\frac{\partial u}{\partial \xi} = -m(\xi)u - ku\int_{\eta \in J(\xi)} v(\eta, t)\, d\eta, \tag{4}$$



**Fig. 7** The intervals $J(\xi)$ and $I(\eta)$. In the representation above, $J(\xi) : \eta_0(\xi) \leq \eta \leq 1$ and $I(\eta) : 0 \leq \xi \leq \eta_0^{-1}(\eta)$.

which is a partial differential–integral equation for the prey and predator densities. It is accompanied by an initial condition

$$u(0, t) = h(t), \quad t \geq 0, \tag{5}$$

where $h(t)$ is the (nonnegative) density hatched at time $t$ with zero development; for example, $h$ usually has its support in a bounded interval $\tau \leq t \leq \sigma$ where emergence occurs. Equation (4) is a reaction-advection equation that propagates signals at the speed $r(\theta(t))$ of prey development, with a nonlocal reaction, or sink, term depending upon the integrated predator density.

As a point of interest we also observe that (4) can be written in the form

$$\frac{\partial u}{\partial t} + r\big(\theta(t)\big)\frac{\partial u}{\partial \xi} = -m(\xi)u - ku \int_0^1 K(\xi, \eta)v(\eta, t)\, d\eta, \tag{6}$$

where the kernel $K$ is defined in terms of $\eta_0$ by

$$K(\xi, \eta) = \begin{cases} 0, & 0 \leq \eta \leq \eta_0(\xi), \\ 1, & \eta_0(\xi) < \eta \leq 1. \end{cases} \tag{7}$$

Equation (6) may generalized in various directions. The per capita natural mortality rate $m$ may also depend upon time $t$, population density $u$, total population $U(t) = \int_0^1 u(\xi, t)\, d\xi$, temperature, or other quantities. A more general functional response may be taken for a predation rate, and a diffusion term involving $u_{\xi\xi}$ can be added to the left side of (6) to represent natural variability in development of a cohort. We note that functional responses that include handling times are extremely complex.

### 3.2. The predator equation

The dynamics for the predator population can be determined in a similar manner, with careful attention paid to the form of the predation rate. Because we are formulating a cohort model, the predation term does not produce additional predators but rather serves only to decrease the predators' natural mortality rate. Following a similar argument for the predator, as in Section 3.1, we have

$$\frac{\partial v}{\partial t} + \rho\big(\theta(t)\big)\frac{\partial v}{\partial \eta} = -n(\eta)v + k'v \int_{\xi \in I(\eta)} u(\xi, t)\, d\xi.$$

Here, the predation rate is $k'v(\eta, t)U(\eta, t)$, where $k'$ is the rate constant and

$$U(\eta, t) = \int_{\xi \in I(\eta)} u(\xi, t)\, d\xi$$

is the total number of prey that may be consumed by predators of size $\eta$, and where

$$I(\eta) = \big\{\xi : (\xi, \eta) \in E\big\}$$

is the interval of prey sizes attacked by predators of size $\eta$ (see Fig. 7). The local balance law for the predators can be written

$$\frac{\partial v}{\partial t} + \rho\big(\theta(t)\big)\frac{\partial v}{\partial \eta} = -n(\eta)v + k'v\int_0^1 L(\xi, \eta)u(\xi, t)\,d\xi, \tag{8}$$

where the kernel $L$ is given by

$$L(\xi, \eta) = \begin{cases} 1, & 0 \leq \xi \leq \eta_0^{-1}(\eta), \\ 0, & \eta_0^{-1}(\eta) < \xi \leq 1. \end{cases} \tag{9}$$

In this case, we append a boundary condition

$$v(0, t) = g(t), \quad t \geq 0, \tag{10}$$

where $g(t)$ is the emerging predator density with zero development.

Because $\xi$ and $\eta$ are development coordinates we can replace them by the generic variable $z$. Then, Eqs. (6) and (8) governing the densities $u(z, t)$ and $v(z, t)$ can be written

$$\frac{\partial u}{\partial t} + r\big(\theta(t)\big)\frac{\partial u}{\partial z} = -m(z)u - ku\int_0^1 K(z, \eta)v(\eta, t)\,d\eta, \tag{11}$$

$$\frac{\partial v}{\partial t} + \rho\big(\theta(t)\big)\frac{\partial v}{\partial z} = -n(z)v + k'v\int_0^1 L(\xi, z)u(\xi, t)\,d\xi, \tag{12}$$

$t > 0$, $0 < z < 1$, where the kernels $K$ and $L$ are defined in (7) and (9). Observe that when we move to a single variable $z$ the region $E$ of interaction is hidden in the kernels $K$ and $L$. Equations (11), (12) are the fundamental equations. They form a highly complex development-structured model. In general, numerical methods are required to solve them.

However, under some simplifying assumptions about the development rate, the temperature variation, and the form of the mortality rate, the population model (11), (12) can to some degree be resolved into a simpler analytical model by the method of characteristics (Logan, 1994, 2006; Kot, 2000; Allen, 2007). To this end, (11), (12) are equivalent to a coupled system of ordinary differential-integral equations, the characteristic system

$$\frac{du}{dt} = -m(z)u - ku\int_0^1 K(z, \eta)v(\eta, t)\,d\eta \quad \text{on } \frac{dz}{dt} = r\big(\theta(t)\big), \tag{13}$$

$$\frac{dv}{dt} = -n(z)v + k'v\int_0^1 L(\xi, z)u(\xi, t)\,d\xi \quad \text{on } \frac{dz}{dt} = \rho\big(\theta(t)\big). \tag{14}$$

Hence, the partial differential operators reduce to ordinary differential operators on the cohort paths (characteristics). In theory, these equations can be integrated, along with the boundary conditions, to determine how the population densities $u$ and $v$ vary as functions of $t$ along the cohort paths. The characteristic equations provide a starting point for analytic studies, and they also provide a vehicle to numerical algorithms (characteristic methods, hybrid methods).

*Remark 2.* Part of what makes the model (11) and (12) especially tractable is that the development rates depend only upon the given temperature history, which depends upon time. Therefore, the simple advection operators in (11) and (12) are known a priori and the characteristics (cohort paths) can be determined in advance. In some applications, the development rate of the variable $z$ could depend upon both $t$ and $z$, giving a more complicated operator of the form

$$\frac{\partial u}{\partial t} + \frac{\partial}{\partial z}\big(g(z,t)u\big),$$

where $\frac{dz}{dt} = g(z,t)$ is the growth rate. In the von Bertalanffy growth law, for example, $g(z,t) = a(t)z^2 - bz^3$, where $z$ is a suitable length measurement and $a = a(t)$ is related to the feeding rate.

## 4. Nonstructured predator dynamics

As in the case of most, all structured models discussed in the literature, analytical progress can be made only under simplifying assumptions, the main one being that one of the species is unstructured. We opt for this type of strategy in this section, where a structured predator density is imposed, or the predator density is defined by a temporal differential equation without structure. Also, the predator and prey roles can be reversed and the prey population can be imposed. Actually, these are important cases because, in many inter-actions, for example, when the predator is a generalist feeder, the predator is basically unaffected by the prey population. In these cases, it is reasonable to impose a predator density upon the development-time space of the prey. Alternately, the prey may be a plant species undergoing no development while being preyed upon by a developing insect herbivore.

For a specific example, in experiments on wandering wolf spiders (*lycosa*) and grasshoppers (e.g., *M. sanguinipus*) in grassland ecosystems (Joern et al., 2006), it was found that spider density was more or less uniform across a summer growing season, both in size and number. Because spiders are generalists, their population is unaffected by grasshopper densities; so, it is reasonable to assume the predator density is constant across the development period. Migrating birds and robber flies are also grasshopper predators (see Joern and Gaines, 1990). Robber flies, for example, are aggressive, generalist, preda-cious insects that emerge as flying adults from their larval-pupal stages. After emergence, we can assume they are present in the adult stage throughout the development period of the grasshopper and that they are subject only to natural mortality, independent of the grasshopper population. Therefore, we can model the robber fly density, for example, as an exponentially decreasing function of time.

In general, the imposed predator density may be constant, a given function of time $t$, a given function of both $z$ and $t$, for example, perhaps a traveling wave form $v = \phi(z - ct)$.

If we prescribe predator densities, only the first equation in (13), (14) comes into play:

$$\frac{du}{dt} = -m(z)u - ku \int_0^1 K(z,\eta)v(\eta,t)\,d\eta, \qquad \frac{dz}{dt} = r\big(\theta(t)\big), \tag{15}$$

where $v(z,t)$ is given. In this case the right side of the equation, or source term, is linear in $u$ with a coefficient that depends upon $z$ and $t$. It therefore takes the form

$$\frac{du}{dt} = -\mu(z,t)u \quad \text{on} \quad \frac{dz}{dt} = r(\theta(t)), \tag{16}$$

where

$$\mu(z,t) = m(z) + k \int_{\eta_0(z)}^{1} v(\eta,t)\,d\eta, \tag{17}$$

where $\eta_0(z)$ is defined as the lower boundary of $E$ (see Fig. 4). Without loss of generality, we assume the time of the first cohort is $\tau = 0$. Because there are no prey at time $t = 0$, it is clear that the population density is zero in the region preceding the first cohort path. To obtain the density in region ahead of the first cohort path, we first parameterize the boundary data at $z = 0$ by

$$t = \tau, \qquad u = h(\tau) \quad \text{at } z = 0. \tag{18}$$

The cohort curves in this region are calculated by integrating the second equation in (16) to obtain (see Eq. (2))

$$z = \xi(t;\tau), \quad t \geq \tau \geq 0. \tag{19}$$

Integrating the first equation in (16) with $z = \xi(t;\tau)$ gives

$$\int_{h(\tau)}^{u} \frac{du}{u} = -\int_{\tau}^{t} \mu(\xi(s;\tau),s)\,ds,$$

which reduces to

$$u = h(\tau)\exp\left\{-\int_{\tau}^{t} \mu(\xi(s;\tau),s)\,ds\right\}, \quad \text{for } z \leq \xi(t;\tau),\ t > 0. \tag{20}$$

This is a parametric form of the prey density in terms of the parameter $\tau$, which is the emergence time. The explicit form of the solution $u = u(z,t)$ in terms of the development-time variables $(z,t)$ is given by (20), after substituting $\tau = \tau(z,t)$, which is found from solving $z = \xi(t;\tau)$ for $\tau$.

Practically, one method to obtain the solution surface $u(z,t)$ is to numerically solve $z = \xi(t;\tau)$ for $\tau$ for a lattice of points $(z,t)$ in the $zt$ plane, and then substitute those values into (20). Or, the solution of (20) can be obtained by a numerical algorithm (a finite difference method, or a hybrid finite difference-characteristic method) for solving partial differential equations.

There are some interesting cases where the characteristics (cohort paths) may be found explicitly.

1. When the development rate is constant, i.e., $dz/dt = b$, then $z = b(t - \tau)$, which are straight lines. This is the case that prey development is independent of temperature.
2. When the development rate is linear in time, i.e., $dz/dt = at + b$, then $z = \frac{a}{2}(t - \tau)^2 + b(t - \tau)$, which is a family of parabolas. See Example 1 for a discussion of this case.

In each of these cases, one can find $\tau = \tau(z, t)$ explicitly and write down the solution (20) in closed form.

*Example 2.* (Time-dependent predator density) For illustration, we consider the special case when the predator density $v$ is time-dependent, the prey mortality rate is constant, and $\eta_0$ is a specific function:

$$m(z) = m_0, \qquad \eta_0(z) = z, \qquad v(z, t) = V(t).$$

Then (17) becomes

$$\mu(z, t) = m_0 + kV(t)(1 - z).$$

Hence,

$$\int_{\tau}^{t} \mu(z, s)\, ds = \int_{\tau}^{t} \left[ m_0 + kV(s)\big(1 - \xi(s, \tau)\big) \right] ds,$$

which, from (20), yields the solution.

*Example 3.* (Constant predator density) In this case the integral (20) may be calculated explicitly, leading to a formula for the solution. If $V(t) = v_0$ with constant development rate, $z = b(t - \tau)$, we get

$$\int_{\tau}^{t} \mu(z, s)\, ds = (m_0 + kv_0)(t - \tau) - \frac{kv_0 b}{2}(t - \tau)^2.$$

From (20), the solution is given by

$$u = h(\tau) \exp\left[ -(m_0 + kv_0)(t - \tau) + \frac{kv_0 b}{2}(t - \tau)^2 \right]$$

$$= h(t - z/b) \exp\left[ -(m_0 + kv_0)z/b + \frac{kv_0 b}{2}(z/b)^2 \right].$$

Therefore, the fixed-time profiles of the solution, as functions of development, decay exponentially (because $m_0 + kv_0 > kv_0/2$, the decay term dominates the quadratic). See Fig. 8. In the context of a global temperature change, the predator-prey interaction can be reduced or be increased only through altered prey emergence periods or altered nymphal periods. Here we are assuming the prey cohort emerges in a finite interval $0 \le t \le \tau$, so $h(t) = 0$ for $t > \tau$. An increased temperature may cause the emergence interval to contract and the prey will speed through development more rapidly, having a shorter nymphal period; this will decrease the predation effect. On the other hand, lower temperatures may stretch the emergence interval and lengthen the nymphal period, leading to increased predation and lower prey densities. Thus, in this case of constant predator density, higher temperatures favor the prey and lower temperatures favor the predator. This supports the conclusion put forth in the case of grasshoppers and spiders (see Logan et al., 2006; Joern et al., 2006). This case is also applicable to grasshoppers, for example, that are preyed upon during a given period of time by migratory birds. Temperature change can offset the arrival times and thus the period of predation.
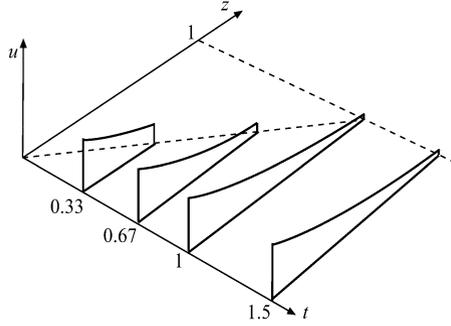
**Fig. 8** Time snapshots of the solution (21) at four fixed times $t$. The leading cohort curve (dashed), or characteristic, emanating from the origin carries a wave front of prey into development time-space.
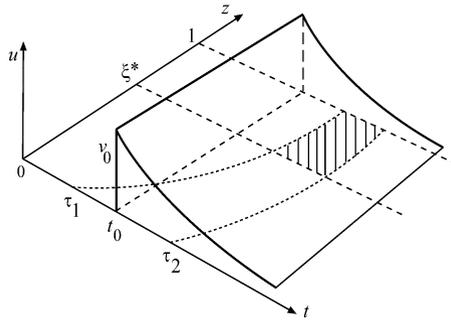


**Fig. 9** The decaying surface represents the density of a cohort of robber flies, the predator, that emerges at time $t = t_0$ and is subject to a constant per capita mortality. A grasshopper cohort emerges in $[\tau_1, \tau_2]$ and proceeds through development along characteristics. Predation occurs in the shaded region where $z \geq \xi^*$ because all predators (adults) consume only prey of size $z \geq \xi^*$, which defines the region $E$. The temperature dependence in this example arises only in the emergence times.

*Example 4.* Another interesting case that can be resolved analytically occurs when a cohort of adult predators emerges at a fixed time and then decrease in numbers as time increases. We assume the predator density has the form

$$v = V(t) = \begin{cases} 0, & t < t_0, \\ v_0 e^{-\gamma(t-t_0)}, & t \geq t_0. \end{cases}$$

Thus, predators emerge at time $t \geq t_0$ and suffer a constant per capital mortality rate $\gamma$. The subsequent discussion refers to Fig. 9. An example is the interaction between robber flies and grasshoppers. The grasshoppers emerge during an interval of time ($\tau_1 \leq t \leq \tau_2$) and progress toward maturity through a series of instars. Robber flies are assumed to emerge from the pupal stage as adults, when they become flying, generalist, predacious flies. They emerge at $t = t_0$, their numbers declining over time; there is no development, but rather the adult robber fly population is superimposed upon the development-time coordinates of the grasshopper. Typically, robber flies prey upon the larger instars of the

grasshoppers, which is modeled by the interaction $E : z \geq \xi^*$. The function $\eta_0$ (see Fig. 7) is piecewise constant and given by

$$\eta_0(z) = \begin{cases} 0, & z < \xi^*, \\ 1, & z \geq \xi^*. \end{cases}$$

The solution formula (20) is rather messy in this case, and therefore we show a diagram that illustrates the interaction and gives more insight into the model. Figure 9 shows the surface $v = V(t)$ and the region (shaded) in development-time space where predation occurs. For $z < \xi^*$ there is no predation; it follows that

$$u = u^*(z, t) = h\big(\tau(z, t)\big)e^{-m_0(t-\tau(z,t))}, \quad z < \xi^*.$$

For $z \geq \xi^*$ predation sets in and the governing equation is

$$\frac{du}{dt} = -m_0 u - k v_0 e^{-\gamma(t-t_0)} \quad \text{on } z = \xi(t, \tau),$$

which is accompanied by a boundary condition given along $z = \xi^*$, namely

$$u(\xi^*, t) = u^*(\xi^*, t).$$

We do not write down the solution formula. Rather, we remark on how temperature change affects predation. There are two possibilities: (a) The time parameter $t_0$ can be changed to simulate different emergence times of the cohort of adult robber flies. If $t_0$ is decreased then the predator surface will be shifted left (backward in time) and a smaller density of robber flies interacts with the grasshoppers, leading to less predation. If $t_0$ is increased, then the surface shifts right (forward in time) and higher densities of robber flies are present when the larger grasshopper instars are present; thus there is more predation. (b) The emergence interval $\tau_1 \leq t \leq \tau_2$ of the grasshoppers may shift left or right, or contract or expand; this gives rise to the same effects as in (a). In a real system, both (a) and (b) are likely to occur. The effects may cancel, leading to no change, or they may add, leading to substantial change. Both situations are observed (for examples, see Buse and Good, 1996; Visser and Holleman, 2001; Visser and Both, 2005).

Finally, we note that an imposed predator density $v = V(t)$ may defined by a dynamical law, or differential equation, such as the logistic equation:

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right).$$

For example, Gurtin and Levine (1979) and Saleem (1984) adopt this type of strategy for a case of egg-eating predators.

*Example 5.* Further, the imposed predator density may satisfy a partial differential equation that is not coupled back to the prey equation. In other words, it evolves independently of the prey population. Then

$$\frac{\partial v}{\partial t} + \rho\big(\theta(t)\big)\frac{\partial v}{\partial z} = -n(z)v,$$

where there is only a natural mortality rate. If the boundary condition is given by $v(0, t) = g(t)$, where $t$ is in some emergence interval, then

$$v = g(\kappa) \exp\left(-\int_{\kappa}^{t} n\big(\eta(s, \kappa)\big) ds\right),$$

where $\kappa = \kappa(z, t)$ is found from the differential equation for the cohort paths, $\frac{dz}{dt} = \rho(\theta(t))$, or $z = \eta(t, \kappa)$ with $z = 0$ at $t = \kappa$. Then, the prey equation takes the form of (16).

*Remark 3.* In a similar manner as above, where the predator population density is imposed, we can alter the viewpoint and assume a given prey density while structuring the dynamics of the predator population. A situation where this occurs is in "budburst," where a predator, for example, developing larva of winter moths, consume the buds of oak trees (Buse and Good, 1996; Visser and Holleman, 2001). The larva are developing, but the oak buds can be assumed to be in a constant state of development upon their appearance.

## 5. Summary

We have introduced a continuous time, phenologically-structured, cohort model of predator-prey interaction. The model treats the physiological development of the prey and the predator independently, as functions of temperature. The interaction terms have the form of Lotka–Volterra, or mass-action, kinetics and lead to nonlocal source terms, through which the coupling occurs. The full model requires numerical resolution. However, in special cases where one of the species in unstructured, or has a density imposed on the system, some progress can be made in obtaining closed-form, analytic solutions. The model is applicable to an interaction where at least one of the species' development rates is strongly driven by environmental temperatures.

The difference between this model and other structured predator-prey models is the inclusion of temperature dependence. By altering the temperature history, the model can assess the possible changes in interactions and population densities that might occur under climate change. Although not addressed in the equations in this paper, temperature dependence in the natural mortality rates and the functional responses can be included in a straightforward manner. Hopefully, the form of the model can suggest strategies for ecologists to develop appropriate data sets to study phenology changes.

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