INSECT PREDATOR-PREY DYNAMICS AND THE BIOLOGICAL CONTROL OF APHIDS BY LADYBIRDS

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INTRODUCTION

Predators are generally considered to be less effective biological control agents than parasites (DeBach, 1964). The famous exception is the control of the cottony-cushion scale, *Icerya purchasi* Maskell, by the ladybird beetle *Rodolia cardinalis* (Mulsant). This outstanding success resulted in the widespread and haphazard introduction of ladybird beetles. However, aphidophagous species of ladybird beetles have generally proved ineffective biological control agents.

In spite of the long-standing interest in mathematical models of predator-prey population dynamics, there has been little success in using them to account for why insect predators have generally been less effective biological control agents than parasitoids (Beddington *et al.*, 1976, 1978; Hassell, 1978; Godfray and Hassell, 1987; Murdoch 1994). Here we offer an explanation as to why insect predators have little effect on the dynamics of their prey. We propose a population dynamics model that incorporates optimization of egg distribution rather than the usually used functional response as the principal force driving predator dynamics. In this model, the predator's oviposition strategy is determined by bottlenecks in the availability of prey that occur during the development of the predator's offspring. For adults, the finding of oviposition sites is assumed to be more important than the functional response to prey. Furthermore, if the ratio of the developmental time of the predator to that of its prey ("generation time ratio," GTR–Kindlmann and Dixon, 1999) is large, then from an evolutionary perspective the predator has to "project" far into the future. If the existence of a patch of prey is limited in time, then it is advantageous for the predators to lay eggs early in the existence of a patch, as future prey availability is uncertain. This uncertainty also makes cannibalism advantageous. Because of the risk of cannibalism, predators tend to lay fewer eggs in a patch, but continue to oviposit until cues indicate that it is highly likely that their eggs will be eaten by conspecific larvae. This is when the "egg window" closes and ovipositing predators abandon the prey patch. Cannibalism thus acts to regulate the numbers of predators per patch (Mills, 1982)

THE PREDATOR–PREY MODEL

Biological Assumptions

Insect herbivores have frequently been observed to first increase and then decline in abundance, even in the absence of natural enemies (Dixon, 1997, 2000). Such declines are often caused by emigration from patches when the prey disperses to find new vacant patches. The prey individuals respond negatively to their cumulative density. Thus in our model, the regulatory term for prey, when alone, is its cumulative density, *h*, instead of some function of its instantaneous density. In contrast to the logistic or exponential growth models, this function allows prey to decline in abundance with increasing time even in the absence of natural enemies.

In most insect predator-prey systems, the generation time ratio, GTR, is large, and the developmental time of the predator is comparable with the duration of a patch of prey (Dixon, 2000). Therefore, as explained above, there is strong selection pressure on a predator to lay its eggs early in the development of a patch of prey (Hemptinne *et al.*, 1992). Predators born in a patch rarely reproduce within the same patch (Dixon, 2000), but after completing their development fly off and reproduce elsewhere. Therefore we assume that (1) the initial density of the predator in a patch is defined by the number of eggs laid there by adults that developed in other patches of prey, arrived to this patch, and reproduced there during the "egg window," and (2) changes over time in the number of predators within a patch are due to larval cannibalism and not reproduction.

We assume the predator is cannibalistic but has a preference, *p*, for eating prey, as opposed to conspecifics. If they prefer prey, then *p* > 1, but *p* may also be less than one, as for example when the larvae of a predator prefer to eat conspecific eggs, which cannot defend themselves. If *p* = 1, the predator shows no preference for either prey or conspecifics (the "meet and eat" hypothesis).

Between-season dynamics are to a large extent determined by the within-season dynamics. For simplicity, we assume the predator is univoltine and its prey achieves only one peak in abundance during a season. The number of prey next spring is calculated by multiplying the autumn number by winter mortality, and the number of predators is calculated by multiplying the autumn number by winter mortality and predator fecundity. Between seasons both prey and predators redistribute themselves among the many patches that make up the population.

Within-Season Dynamics

Based on the above biological assumptions, Kindlmann and Dixon (1993) and Kindlmann *et al.* (2002) showed that the within-season dynamics of this predator-prey system can be described by the following set of differential equations:

$$\frac{dh}{dt} = ax, \qquad\qquad h(0) = 0, \qquad\qquad (1a)$$

$$\frac{dx}{dt} = (r - h)x - \frac{vpxy}{b + px + y}, \qquad x(0) = x_0, \qquad (1b)$$

$$\frac{dy}{dt} = -\frac{vy^2}{b + px + y}, \qquad\qquad y(0) = y_0, \qquad (1c)$$

where

    h(t)   - cumulative density of the prey at time t
    x(t)   - density of prey at time t
    a   - scaling constant relating prey cumulative density to its own dynamics
    r   - maximum potential growth rate of the prey
    y(t)   - density of predator at time t
    v   - predator voracity
    b   - parameter of the functional response of the predator
    p   - predator's preference for prey
    T   - time when predator matures; coincides with the duration of a patch of prey,
             yielding initial values x(T) and y(T) for the next season.

Equation (1a) describes changes in cumulative density of prey, (1b) describes changes in prey density, and (1c) describes the decrease in predator density due to cannibalism. A typical trend in numbers in a patch predicted by model (1) is shown in Fig. 1. There is no predator reproduction in the patch; therefore, predator numbers monotonously decline. As a consequence, if prey abundance (x) increases at the beginning (i.e., if y_0 is sufficiently small, so that $\lim\limits_{t \to 0+} \dfrac{dx}{dt} < 0$)then as time proceeds the dynamics of the prey is less and less influenced by the declining numbers of the predator. Because of the way the diet of the predator is defined (the terms containing v in [1b] and [1c]), the decline in predator numbers is more pronounced when there are few prey individuals relative to predator individuals. That is, when the ratio x/y is small at the beginning and when prey numbers have passed their peak and become small again due to the negative effect of cumulative density. Predators have almost no influence on the prey dynamics in this system (Kindlmann and Dixon, 1993). Not surprisingly, the number of predators that survive is positively influenced by the initial number of prey and negatively influenced by the initial number of predators (Kindlmann *et al.*, unpub.).

The predicted trends in abundance (Fig. 1) closely match those observed in nature in aphids (Dixon *et al.*, 1996; Kindlmann and Dixon, 1996, 1997; Dixon and Kindlmann, 1998; Kindlmann *et al.*, 2002) and ladybird beetles (Osawa, 1993; Hironori and Katsuhiro, 1997; Yasuda and Ohnuma, 1999; Kindlmann *et al.*, 2000; Yasuda *et al.*, 2002).
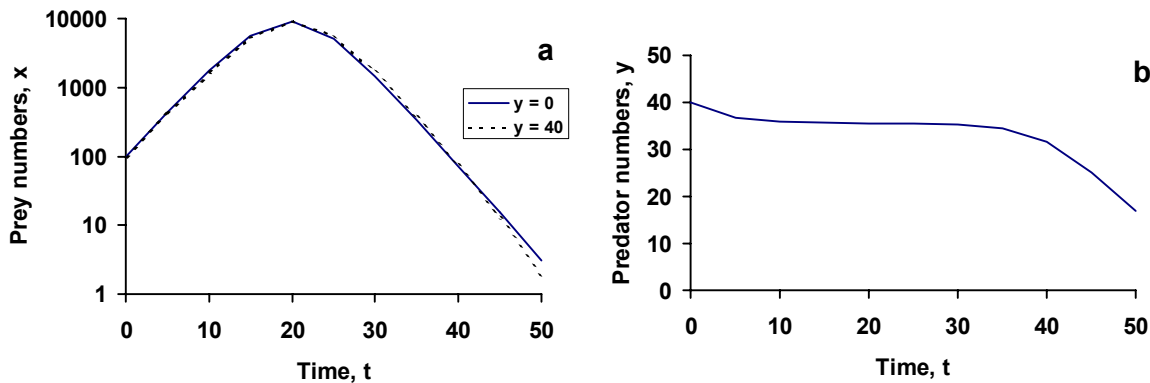

Figure 1. Trends in time in prey (a) and predator (b) abundance predicted by the model when $a = 0.000005$, $r = 0.3$, $v = 1$, $b = 0$, $p = 1$, $x_0 = 100$, $y_0 = 0$ and $y_0 = 40$. In (a) prey density in the absence of predators and the presence of 40 predators (see inset for line code) is also presented.

Figure 2 shows the predicted final numbers of prey and predators relative to their initial numbers predicted by the model (1) for different initial values of prey and predator numbers. Independently of the choice of the parameters a, v, b, p and T, there is a strong inverse relationship between the final and initial number of prey (Fig. 2a). The dependence between the final number of prey and the initial number of predators is much weaker (Fig. 2b), almost linear on a log-log scale with the slope dependent on the initial numbers of prey. The dependence of the final number of predators on the initial number of prey (Fig. 2d) resembles a power function with the exponent smaller than, but very close to 1 and there is a weak dependence of the final number of predators on their initial number (Fig. 2c) compared with that of the final number of predators on the initial number of prey.
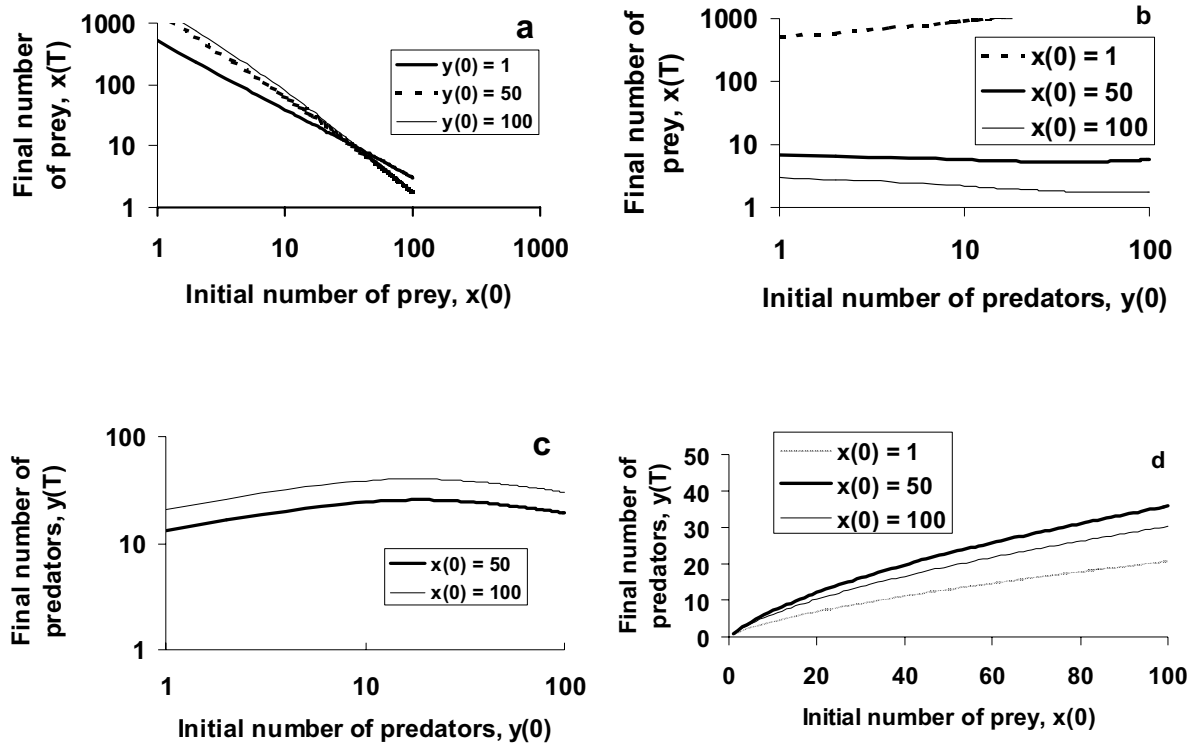
Figure 2. Predicted relationships between final and initial numbers of prey and predator, as predicted by the model (1). Parameter values: $r = 0.3$, $a = 0.000005$, $v = 1$, $b = 0$, $p = 1$.
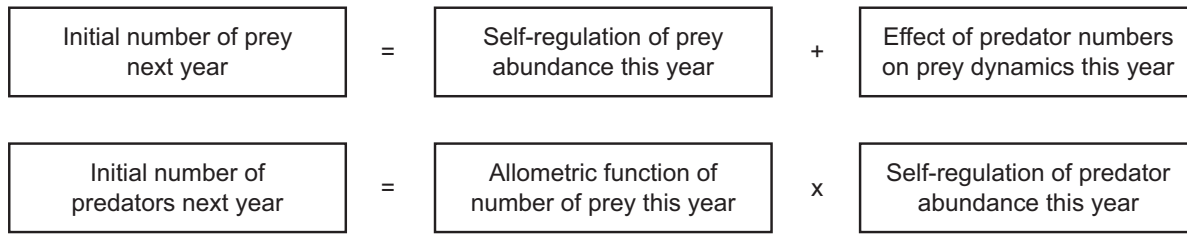
Between-Season Dynamics

The above relations between the initial prey and predator numbers ($x[0]$ and $y[0]$) and their final numbers ($x[T]$ and $y[T]$) within a season can be used to develop a between-season population dynamics model for the simple case where all patches are the same, and the number of patches (n) is the same every year (Kindlmann *et al.*, unpub.). If we denote the total number of prey and the total number of predators in a population consisting of n patches at the beginning of the year t, by x_t and y_t, respectively, and if $x_t = n. x(0)$ and $y_t = n. y(0)$, then $x_{t+1} = n.d_x.x(T)$ and $y_{t+1} = n. d_y.f. y(T)$, where d_x and d_y are the probabilities of prey and predators, respectively, surviving from the end of one season to the beginning of the next and f is predator fecundity.

It is not possible to derive the exact relations between x_t and y_t and x_{t+1} and y_{t+1} from model (1), but approximate relations can be estimated from Fig. 2. The notation can be simplified by linearizing the dependence, by making $X_t = \ln(x_t)$ and $Y_t = \ln(y_t)$. This results in the following system of difference equations:

$$X_{t+1} = a_1 - b_1 X_t + (c_1 - d_1 X_t) Y_t$$
$$Y_{t+1} = a_2 X_t^{b_2} / (c_2 Y_t - d_2 Y_t^2) \qquad (2)$$

Biologically:

Initial number of prey next year	=	Self-regulation of prey abundance this year	+	Effect of predator numbers on prey dynamics this year
Initial number of predators next year	=	Allometric function of number of prey this year	x	Self-regulation of predator abundance this year

In this system when predators are absent, the number of prey next year increases when the number of prey this year is low, but is strongly regulated by itself ($X_{t+1} = a_1 - b_1 X_t$). Influence of the predator on prey dynamics (the term $[c_1 - d_1 X_t].Y_t$) depends on the sign of the term $c_1 - d_1 X_t$. It can be negative and directly proportional to the number of predators, Y_t. However, when the number of prey the preceding year is very low, so that $c_1 - d_1 X_t > 0$, predators may affect the number of prey this year even positively. This counterintuitive result follows from the fact that predators by eating prey early in the season reduce their numbers, and so delay the timing of their peak numbers, which "shifts" the curve describing prey population dynamics in Fig. 1a to the right and as a consequence positively influences the final number of prey. The number of predators next year is positively, but less than linearly, influenced by the number of prey this year (see the term   ). The shape of the between-season relation in the number of predators is parabolic, indicating that predators do best at intermediate densities–when there are few predators, few of them survive, and because of cannibalism, few survive even when they are initially numerous.

The types of behavior predicted by this model are shown in Fig. 3. Because of the inverse relationship between x_t and x_{t+1}, prey numbers (X_t) usually tend to oscillate between years, while the increasing dependence of y_{t+1} on y_t results in a monotonous approach to equilibrium in predator numbers.
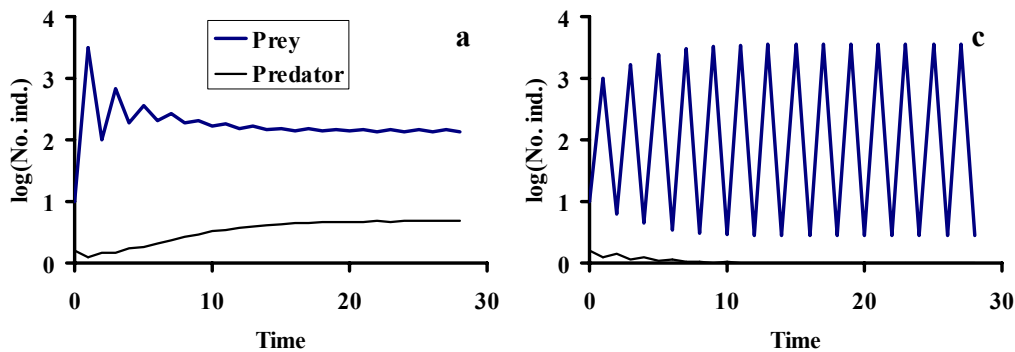

Figure 3. Typical trends in the abundance from year to year of prey and predator predicted by the model. Prey always tends to oscillate from year to year, at least initially, while predator abundance usually monotonously approaches an equilibrium.

To conclude, in situations where the developmental time of the predator is long relative to that of its prey, predators are unlikely to be effective classical biological control agents. This is because the predator abundance is strongly regulated by cannibalism (Kindlmann and Dixon, 2001). This is well illustrated by the aphidophagous ladybird – aphid system.

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