

**Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae)
and its consequences for their use in biological control**

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Abstract. A model optimizing the number of eggs laid in an aphid colony by an adult ladybird reveals that there exists an optimum number, which maximizes the resulting offspring biomass. This remains true even if the model is expanded to include more than one adult ladybird and several aphid colonies. Adult ladybirds should not continue to aggregate in areas of aphid abundance (Kareiva & Odell, 1987), but should leave an aphid aggregate, even though the aphids are still increasing in abundance, as soon as a certain number of eggs are laid and/or larvae are present. If the ladybirds lay the optimal number of eggs, then their offspring have only a slight effect on the peak number of aphids.

INTRODUCTION

Understanding predator foraging strategies is of primary importance for the development of successful biological control. It is assumed that predators do not search at random and that the predation rates are greater in regions where prey are abundant (Dixon, 1959; Hassell, 1978). Kareiva & Odell (1987) proposed a model elucidating the behavioural mechanisms that might enable populations of predators to flow towards regions of high prey density. This results from the predators moving at a constant speed but changing their direction of movement more often when satiated (area restricted search) and that increase in prey density increases the feeding rate and satiation of the predators. They apply their model to the spatial dynamics of an interaction between goldenrod aphids, *Uroleucon nigrotuberculatum* (Olive), and adult ladybird beetles, *Coccinella septempunctata* L., to predict the distribution of ladybirds 1 and 2 days after their release.

Kareiva & Odell's (1987) predictions are in good accord with their empirical data. This indicates that the behavioural mechanisms they have arbitrarily chosen lead to predictions that mimic the initial response of ladybirds to aggregates of aphids. However, they did not show whether this type of behaviour is the optimal one for maximizing ladybird fitness, and it is not possible to extrapolate their predictions beyond the two day period of their experiment. Moreover, certain empirical data (Hemptinne et al., 1992) indicate that in the later stages of aphid colony development Kareiva & Odell's predictions do not hold.

For a complete understanding of the mechanisms governing predator behaviour it is necessary to determine the types of behaviour that maximize predator fitness and are selected for. The first step is to optimize the behaviour of predators in an aphid colony. This

can be done by maximizing the reproductive success of each ladybird in terms of number and size of offspring produced.

In this paper the number of ladybird eggs that gives the maximum biomass at the end of the existence of an aphid colony is determined. As both the offspring size and number are subject to selection, this approach provides an explanation of the adaptive behaviour of ladybirds and other predators with similar behaviour. The predictions are compared with field observations.

THE MODEL

Biological background

Aphid populations generally grow exponentially in the initial phases of development and on reaching a certain critical population density the aphids switch to alate production and/or migration. The switch to migration can be seen as a response to a deterioration in the quality of the host plant or severe intraspecific competition. This switch results in a rapid decline in colony size. The adaptive significance of the response of aphids to their own density and to deterioration in food quality, both of which result in migration, will be discussed by Kindlmann & Dixon (in prep.).

Ladybirds arriving in an aphid colony are faced with an optimization problem, the maximization of offspring production. An aphid colony is a temporary and finite food resource. In addition, other ladybirds may lay eggs in the colony. It is not unreasonable to assume the ladybird larvae show a Holling type II functional response to aphid abundance and that the larvae will eat their conspecifics when aphids become rare. Because each aphid colony only exists for finite period of time the larvae may complete their development but not reproduce in that aphid colony.

The biological constraints and rules given below were chosen so as to best represent the behaviour of ladybirds. They are presented in the form of assumptions, which are incorporated in an optimization model. Behaviour, which also may be subject to selection but does not have a direct effect on the maximization of a ladybird's reproductive fitness, e.g., the foraging behaviour of its larvae, sex ratios etc., was ignored.

The assumptions of the model:

- (A1) Aphid populations grow exponentially with a growth rate r , which is the difference between the birth rate, b , and the death rate, d . The aphid population biomass is $x_b(t) = x_s x(t)$, in which aphid size, X_s , is assumed to be constant, whereas the aphid density, x , changes in time.
- (A2) Density dependence comes into effect after a critical density is reached. When the aphid population exceeds the critical density, x_{crit} , the individuals switch to alate production and/or migration at the same rate, b . This switch, however, is not instantaneous and is described by the switch function, $g(t) = e^{vt}/(e^{vT} + e^{vt})$ – see Fig. 1c.
- (A3) The total biomass per unit area of ladybird larvae at time t is $y_b(t) = y(t) \cdot y_s(t)$. Thus, both their size, y_s , and their density, y , may change in time. However, the changes in density, y , are due to cannibalism, as they do not reproduce.

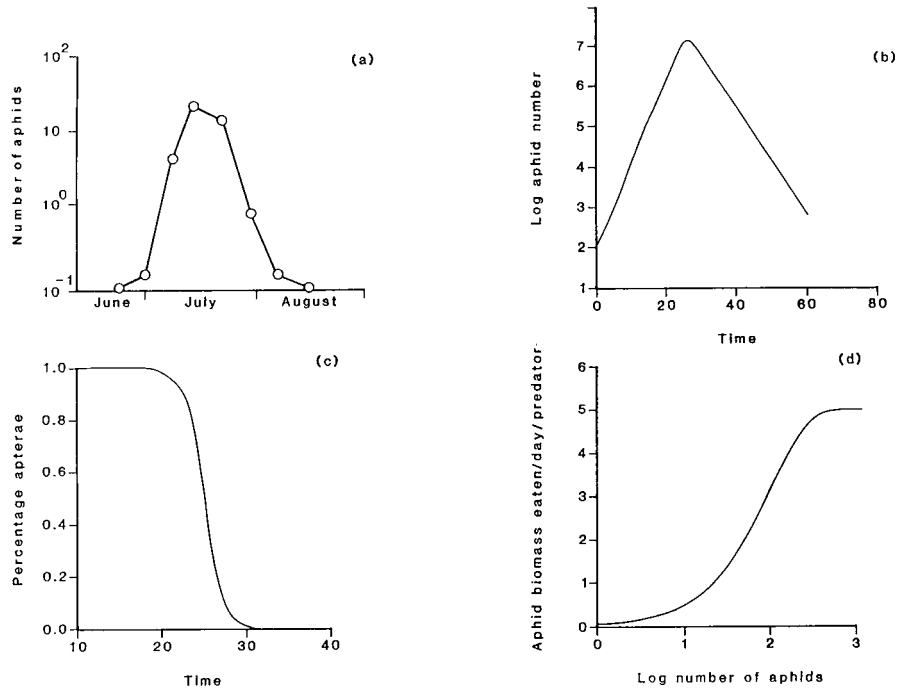


Fig. 1. a) Empirical data on the population dynamics of an aphid colony – after Kareiva (1986); b) Population dynamics of aphid colonies, without predators, as predicted by the model (1); c) Function g [eq. (5)], describing the switch from aptera to alate production; d) Functional response of ladybirds to aphid density. See Table 1 for the parameter values.

- (A4) The functional response shown by ladybird larvae (biomass eaten per predator per unit time) is of Holling type II, described by $f(x, y, y_s) = m \cdot y_s [1 - e^{-a(x+y)}]$ – see Fig. 1d.
- (A5) The larvae attack aphids and conspecifics at random, but prefer aphids with the preference factor p . Therefore, the proportion of aphids in their diet is $p_x = x/(x + y/p)$ and that of the conspecifics is $p_y = y/[p \cdot (x + y/p)]$.
- (A6) The biomass eaten by the larvae is converted into their biomass with a conversion efficiency of q .

Model equations:

Assumptions (A1)–(A6) lead to a set of algebraic and differential equations:

$$x' = (bg - d)x - p_x y f \quad (1)$$

$$y' = -p_y y f \quad (2)$$

$$y_s' = qf \quad (3)$$

$$x_b = x x_s \quad (4a)$$

$$y_b = y y_s \quad (4b)$$

$$g(t) = 1 - \frac{e^{vt}}{e^{vT} + e^{vt}} \quad (5)$$

$$f(x, y, y_s) = m \cdot y_s [1 - e^{-a(x+y)}] \quad (6)$$

$$p_x = \frac{x}{x + y/p} \quad (7a)$$

$$p_y = \frac{y}{p(x + y/p)} \quad (7b)$$

where (1) describes the aphid population dynamics, (2) and (3) the changes in numbers of ladybird larvae and in the size of individual larvae, respectively, and (4) defines the corresponding biomasses of aphids and ladybirds. In eq. (1)–(4) the switch to alate production is expressed by (5), the functional response of ladybird larvae by (6), while (7) describes the ladybird larval preference for aphids as opposed to conspecifics.

Simulations were performed using a range of parameter values (Table 1), which either included all the possible values (q), most of the possible values ($p, y_0, y_s(0), a, m$) or were varied by the choice of units (t, x_s, x_0) or only realistic values were chosen (b, d, T, v).

TABLE 1. Values of the parameters and the functions used in the model. The values of the functions are dependent on the terms in the brackets.

Notation	Description	Range of values used
t	time	0–60
x_s	biomass of one aphid	1
$x(t)$	density of aphid population at time t	
x_0	aphid density at the time of ladybird arrival	100
$x_b(t)$	biomass of the aphid population	
r	growth rate of aphid population	
b	birth rate of aphid population	0.8
d	death rate of aphid population	0.3
x_{crit}	the critical density of aphids above which alates and migration occurs	
$T(x_{crit})$	mean time of the switch to alate production	25
v	velocity of the switch to alate production	1
$g(t, T, v)$	function describing the switch to alate production	
$y_s(t)$	biomass of a ladybird larva	
$y_s(0)$	biomass of a newborn ladybird larva	1–10
$y(t)$	density of ladybirds	
y_0	initial ladybird density	0–40
$y_b(t)$	biomass of ladybird population	
$f(x, y, y_s, m, a)$	the functional response of ladybird larvae	
my_s	aphid biomass necessary for satiation of larvae of size	0.5–2.5
a	parameter determining the shape of the functional response	0.001–0.1
q	efficiency of converting aphid biomass eaten into ladybird biomass	0.01–1
p	preference for eating aphids as opposed to conspecifics	2–10

For each set of parameters $q, p, y_s(0), a, m$, a brute force optimization was performed, maximizing y_b at the end of the existence of the aphid colony ($t = 60$) with respect to y_0 , which was allowed to vary from 0 to 40. For simulations of (1)–(4), Euler method with a step of 0.0001 was used on an HP Apollo computer using a FORTRAN routine. A brute force method was used because there was no a priori information on the behaviour of the

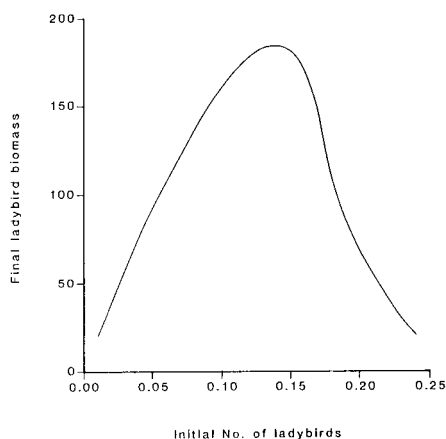


Fig. 2. Ladybird biomass production, y_b , in relation to the initial number of ladybirds, as predicted by the model (1)–(4).

$y_b(y_0)$ function. The use of a small step was crucial, as large steps yielded instability. Values of y_0 larger than 40 were excluded, as they led to a further monotonic decline in the resultant biomass of ladybirds produced.

RESULTS

The values of the parameters $y_s(0)$, m and q did not significantly influence the outcome and therefore the simulation results are given only for one value of these parameters. All the simulations resulted in a common prediction: there is an optimum number of ladybird larvae, which maximizes the biomass production of ladybird larvae at the end of the existence of the aphid colony. The typical situation is depicted in Fig. 2. The sharp increase in ladybird biomass is followed by a sharp decline, when the optimum initial number of larvae is exceeded. This indicates that there should be a strong selection pressure for ladybirds to optimize the initial number of larvae.

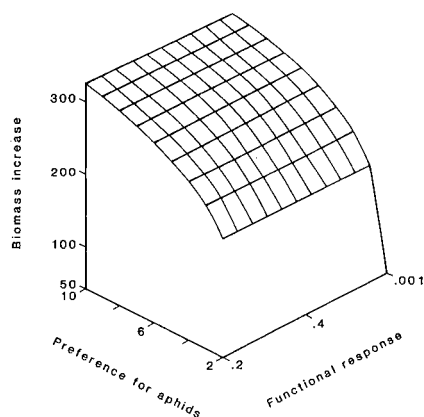


Fig. 3. Increase in the biomass of ladybirds during the existence of the aphid colony, as predicted by the model (1)–(4) for the range of parameter values given in Table 1.

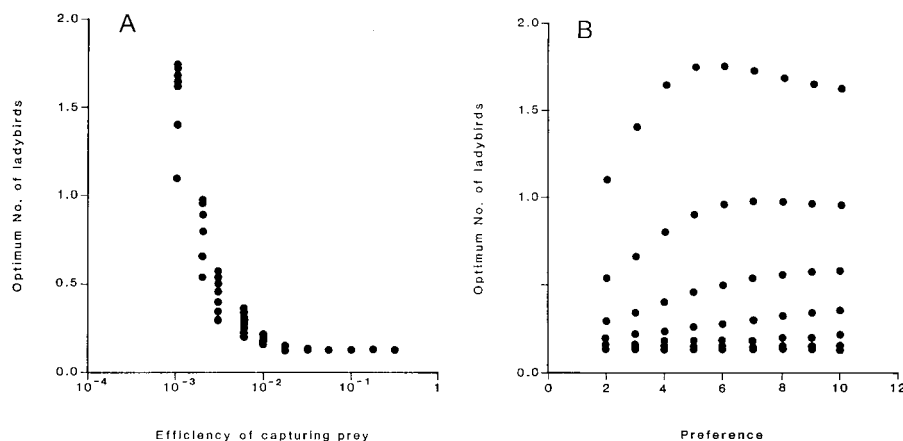


Fig. 4. Optimum initial number of ladybird larvae, as predicted by the model (1)–(4) for the range of parameter values given in Table 1; dependent on (A) the initial slope of the functional response and (B) on the larval preference for aphids.

Outputs of simulations using various values of the parameters p and a are given in Fig. 3 (the increase in biomass of ladybird larvae during the existence of an aphid colony), in Fig. 4 (the optimum number of ladybird larvae per colony) and in Fig. 5 (the ratio of the logarithms of the peak numbers of aphids when the optimum number of ladybird larvae and no larvae are present). An increase in the preference of the larvae for eating aphids (reduction in cannibalism) results in an increase in biomass of ladybird larvae during the existence of an aphid colony (Fig. 3), and an increase in the initial slope of the functional response of the larvae results in a decline in the optimum number of larvae (Fig. 4), and decrease in biomass of ladybird larvae (Fig. 3). Neither of these parameters had a significant effect on the ratio of the logarithms of the peak numbers of aphids when the optimum number of ladybird larvae and no larvae are present.

The most striking result is that if the initial number of larvae is maximized in terms of ladybird biomass production then there is only a slight reduction in the peak number of aphids (Fig. 5). Therefore, if ladybirds are behaving optimally, they should not substantially reduce the size of aphid colonies.

Accepting the above argument Kareiva & Odell's (1987) model can be made more realistic by adding terms describing adult ladybird long term behaviour, that is, some factor that reflects their ability to assess the present and future quality of an aphid colony for their larvae. The accord with empirical data cited by Kareiva & Odell (1987) was due to the short timespan (2 days), for which the ladybirds were observed.

DISCUSSION

The model presented here is of a simple situation, that when no other aphid colonies are available. The existence of other aphid colonies is also likely to affect the behaviour of

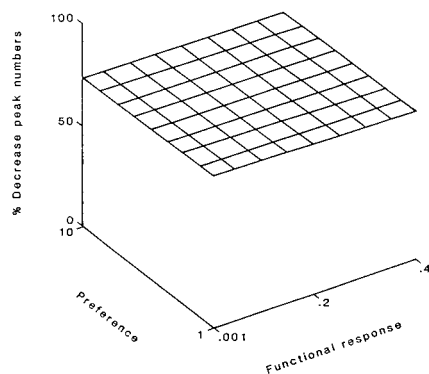


Fig. 5. Decrease in the log of the peak aphid numbers, as predicted by the model (1)–(4) for the range of parameter values given in Table 1.

adult ladybirds. An appropriate tool for studying such a system is the foraging theory patch model of Stephens & Krebs (1986). The patch model predicts that the optimal number of ladybird eggs laid in a particular aphid colony should be lower, when other aphid colonies are available. The main conclusion of this study is that there should be a strong selection pressure optimizing the number of larvae in each aphid colony and that predator pressure will not affect peak numbers of aphids substantially. This conclusion remains valid even when considering more realistic multi-patch systems. The same result is also obtained if there is competition between ladybird adults for aphid prey.

The development and optimization of larval cannibalism is not included in this model, because it deals with the optimization of larval behaviour, not adult behaviour. Larval cannibalism can be seen as an adaptation to an unpredictable environment: adults are not able, accurately, to assess the future growth rate of the aphids as it is, e.g., not able to predict weather. Therefore, the optimum number of larvae is “readjusted” later by cannibalism.

In nature, ladybirds sometimes reduce the abundance of aphids quite dramatically. However, the model indicates that this should be seen as suboptimal behaviour, which is a consequence of a perturbation leading to a scramble for resources, which results in low ladybird numbers the following year. The reduction factor may also seem unrealistically low, but it is not if one bears in mind that ladybirds sometimes do not behave optimally and that there are also other predators using the same resource. The low optimum number of ladybirds is a consequence of the rapid aphid population growth, which cannot be tracked by the growth of ladybird larvae.

Ladybird developmental time is fairly long and comparable in length to the average time for which an aphid colony exists. It does not make sense to lay eggs in old colonies, as the offspring will not be able to complete their development. Therefore, there is a great selective advantage in adults being able to detect an aphid colony in the early stages of its development. Kareiva & Odell’s (1987) model provides one possible mechanism of how aphid colonies are found. Our simulations start at the instant, when no more ladybird eggs will be laid in a colony, because of the reasons cited above. Thus there is no increase in

the number of larvae in our model after the initial number of eggs has been laid. A possible mechanism by which ladybirds could avoid laying eggs in old aphid colonies is for them not to lay eggs when larvae are present (Hemptinne et al., 1992).

This model of the foraging behaviour of ladybird beetles has revealed that if they forage optimally they should have little effect on aphid abundance. If correct, then it may account for why aphidophagous ladybirds have generally been ineffective biological control agents (Hemptinne & Dixon, 1991).

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