# How do immigration rates affect predator/prey interactions in field crops? Predictions from simple models and an example involving the spread of aphid-borne viruses in sugar beet

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**Abstract**

Sugar beet viruses are spread by aphid populations which are preyed upon by natural enemies. This paper discusses the hypothesis that aphid vector population buildup and the spread of viruses can be decisively affected by early activity of natural enemies, e.g. immigrant adult ladybirds. The hypothesis is analysed with two models of the interaction between aphids and coccinellids. The models are based on exponential growth of aphid populations and on a predator density that depends on the balance between immigration and emigration. In the first model, predator feeding rate is assumed to have a maximum level, $\beta$. Under this assumption, there will be a vector outbreak (defined as exponential growth in the long term) if

$$\beta\left(y_0 + \frac{\delta}{\alpha}\right) < (\alpha + \varepsilon)\left(x_0 + \frac{\gamma}{\alpha}\right)$$

In this threshold rule, $x_0$ is initial aphid density, $y_0$ is initial predator density, $\alpha$ is the relative growth rate of the pest, $\beta$ is the feeding rate of the natural enemy, $\gamma$ is the immigration rate of the pest, $\delta$ is the immigration rate of the natural enemy and $\varepsilon$ is the relative emigration rate of natural enemy. In the second model, mortality by predation is proportional to prey density. In this case there will be an outbreak if

$$\alpha > \kappa\, y^*$$

Here $\kappa$ is the relative mortality rate of aphids per unit of predator density and $y^*$ the equilibrium density of the predator. In this threshold rule, the occurrence of aphid outbreaks is determined by aphid population growth rate, predator searching efficacy, predator immigration and emigration rate, but not by initial densities.

Both models point out a sensitivity to the timing of immigration. In the first model, a sufficiently early immigration of the prey can give it a decisive advance on the predator. In the second model, predators can always catch up with prey

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dynamics, but the parameter quantifying searching efficacy ($\kappa$) may decrease in time as leaf area increases.

Results of field experiments on the spread of viruses in sugar beet are interpreted in the light of the model results. The field observations tend to confirm the concept of a critical predator/prey ratio (Model 1) rather than that of a critical predator density (Model 2), but this conclusion remains tentative because immigration rates are unknown.

**Key words:** Aphids, Coccinellidae, natural enemies, predation, biological control, immigration, emigration, spatial, virus spread, model

## Introduction

Many above ground pests and diseases in annual crops overwinter outside the field, e.g. in other fields or in more or less natural habitats. The timing and intensity of immigration into crops, relative to crop phenology, affect the following spread and damage. Several groups of natural enemies or antagonists of pest and diseases also overwinter outside the field. The timing and intensity of their immigration, in relation to the timing and intensity of pest/pathogen immigration, may determine whether a pest or disease outbreak or biological control will occur. It would be desirable to have quantitative criteria to assess the effects of immigration rates and timing on pest and disease dynamics because such criteria would make it possible to relate trends in pest and disease occurrence in crops to spatial dynamics in the larger context of the entire agroecological landscape (Fig. 1; Galecka 1966). Two questions should be asked:

1. Which criteria (e.g. a predator/prey ratio; Janssen & Sabelis 1992, van der Werf et al. 1994) distinguish situations with and without biological control?
2. How are critical values of such criteria affected by times and rates of immigration and other factors such as crop development stage and weather?

In this paper I use two simple models to explore possible answers to these two questions. Results of these models are expressed as threshold rules that mark the transition from natural control to pest outbreak. The model predictions are compared to field data on the spread of sugar beet viruses by the green peach aphid, *Myzus persicae*. This aphid is preyed upon by a complex of predators and parasitoids. This paper focuses on coccinellids, a predator group known to be capable of reducing aphid population buildup (Hodek et al. 1965, Frazer & Gilbert 1976) and thereby the spread of aphid-transmitted viruses (Ribbands 1963, Kershaw 1965, van der Werf et al. 1992).

In Europe, two yellowing viruses occur in sugar beet. The most prevalent

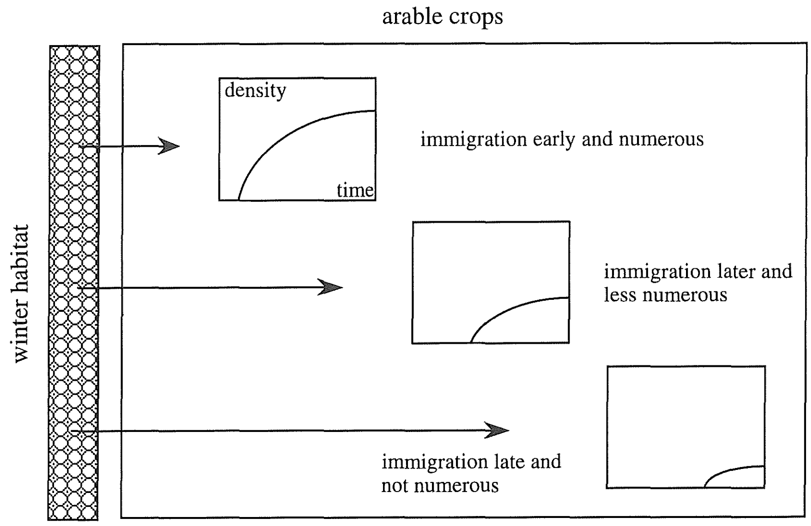


**Fig. 1.** Time and rate of immigration of pests and natural enemies into crops may depend upon distance from overwintering habitats. If migration is a random process, the rate of immigration will rise earlier and to higher levels at short distances from the source than at long distances. The magnitude of these differences and the scale at which they occur depends on circumstances and on species. For instance, *Propylaea quatuordecimpunctata* in an arable field would originate predominantly from nearby overwintering sites (Basedow 1990) whereas in a field experiment with syrphids (Groeger 1992) no differences were observed in time and rate of immigration between sites at different distances, up to 700 m, from an assumed overwintering site.

one is beet mild yellowing virus, BMYV, the other is beet yellows virus, BYV. BMYV belongs to the luteovirus group and is transmitted in the persistent manner. BYV belongs to the closterovirus group and is transmitted in the semi-persistent manner. Upon early and complete infection, sugar beet crops infected with BMYV incur about 30% yield reduction while crops infected with BYV incur 50% yield reduction (Smith & Hallsworth 1990). The two viruses are taxonomically unrelated but their ecologies are similar. Practice considers the two pathogens as a single disease complex (Harrington et al. 1989). The epidemiology of both viruses is characterized by a distinct year cycle. During the crop season, the viruses occur in sugar beet, where they cause leaf yellowing. Their main vector within sugar beet is *M. persicae*. A vector of secondary importance for BYV (but not for BMYV) is the black bean aphid, *Aphis fabae*. During winter, when in Western Europe no beet plants are available in the field, BYV and BMYV occur in a wide range of weedy hosts (Peters 1988). *M. persicae* can overwinter as viviparous females (i.e. anholocyclic) on those weedy hosts, but suffers high mortality. *M. persicae* also overwinters in the form of eggs, produced by sexual males and females (i.e. holocyclic) and then uses woody host plants, such as peach tree, *Prunus persica*, which are not hosts for yellowing viruses. In spring, *M. persicae* populations build up on both types of winter host. In spring and early summer, winged aphids are produced that migrate to (other) weedy hosts. It is during this phase that beet crops become infected. This is called *primary* infection. Infections that are made by aphids dispersing within the crop are called *secondary* infections. Other aphid species than *M. persicae,* e.g. the potato aphid *Macrosiphum euphorbiae*, may play a role in causing primary infections.

In Dutch field crops, three species of coccinellids can rise to abundance levels of significance in aphid control: seven-spot ladybird, *Coccinella septempunctata,* two-spot ladybird, *Adalia bipunctata* and 14-spot ladybird, *Propylea quatuordecimpunctata*, in order of importance. The life-cycle of these species is predominantly univoltine (Hodek 1973, Majerus & Kearns 1989). Adults overwinter in sheltered places, e.g. under leaf litter, in grass tussocks or in bark crevices. They come out of shelter on sunny days in late winter and early spring to forage. Aerial dispersal of adults is frequent throughout spring and summer, so that fresh vegetation, including newly emerged crops with associated aphid populations are colonized at an early stage. Mating and egg laying results in larval populations being abundant in early summer which is the period of highest aphid densities. New adults emerge later in summer. They disperse to hibernation sites in autumn.

*Structure of the paper*

First two simple models are introduced that broadly represent predator/prey dynamics of aphid/ladybird systems in early spring, before ladybird larvae start to make a significant contribution to overall mortality due to predation. Threshold criteria for biological control (defined as the non-occurrence of exponential growth) are derived for both models. These criteria are interpreted in biological terms and the likely importance of timing in both models is shown. Relationships between model parameters and cumulative aphid density, as a measure for pest and vector pressure, are also analysed. Model results are then compared to experiments.

## Models

### Model 1. A prey-predator model with a fixed predator feeding rate and immigration

The model is based on the following set of assumptions:

1. stage differentiation in prey and enemy can be neglected
2. life cycle parameters are constants
3. prey population growth is density-independent
4. the enemy has a fixed feeding rate, independent of density (the plateau of the functional response is taken; this overestimates predation at low prey density)
5. there is constant immigration of both prey and predator
6. prey and predator immigration can start at different times
7. predator emigration is proportional to predator density
8. predators do not reproduce

$$\begin{cases} \dfrac{dx}{dt} = \alpha x - \beta y + \gamma \\ \dfrac{dy}{dt} = \delta - \varepsilon y \end{cases} \tag{1}$$

In these equations, $x$ is pest density, $y$ is predator density, $t$ is time, $\alpha$ is the relative growth rate of the pest ($[x]\,[x]^{-1}\,d^{-1}$), $\beta$ is the feeding rate of the natural enemy ($[x]\,[y]^{-1}\,d^{-1}$), $\gamma$ is immigration rate of pest ($[x]\,d^{-1}$), $\delta$ is the immigration rate of the natural enemy ($[y]\,d^{-1}$) and $\varepsilon$ is the relative emigration rate of natural enemy ($[y]\,[y]^{-1}\,d^{-1}$). $[x]$ and $[y]$ denote dimensions of pest and predator density, e.g. numbers of individuals per $m^2$. The model can be analytically integrated (cf. Edelstein-Keshet 1988, Janssen & Sabelis 1992):

$$\begin{cases} x_t = A e^{\alpha t} - B e^{-\varepsilon t} - C \\ y_t = y^* - (y^* - y_0) e^{-\varepsilon t} \end{cases} \tag{2}$$

where:

$$\begin{aligned} A &= x_0 + B + C \\ B &= \frac{\beta}{\alpha + \varepsilon}(y^* - y_0) \\ C &= \frac{1}{\alpha}(\gamma - \beta y^*) \\ y^* &= \frac{\delta}{\varepsilon} \end{aligned} \tag{3}$$

The predator equation (2) describes a negative exponential convergence from the initial density $y_0$ to an equilibrium density $y^* = \delta/\varepsilon$. The prey equation consists of three terms, of which only the first one increases in magnitude in time. The second term extinguishes exponentially to zero, while the third

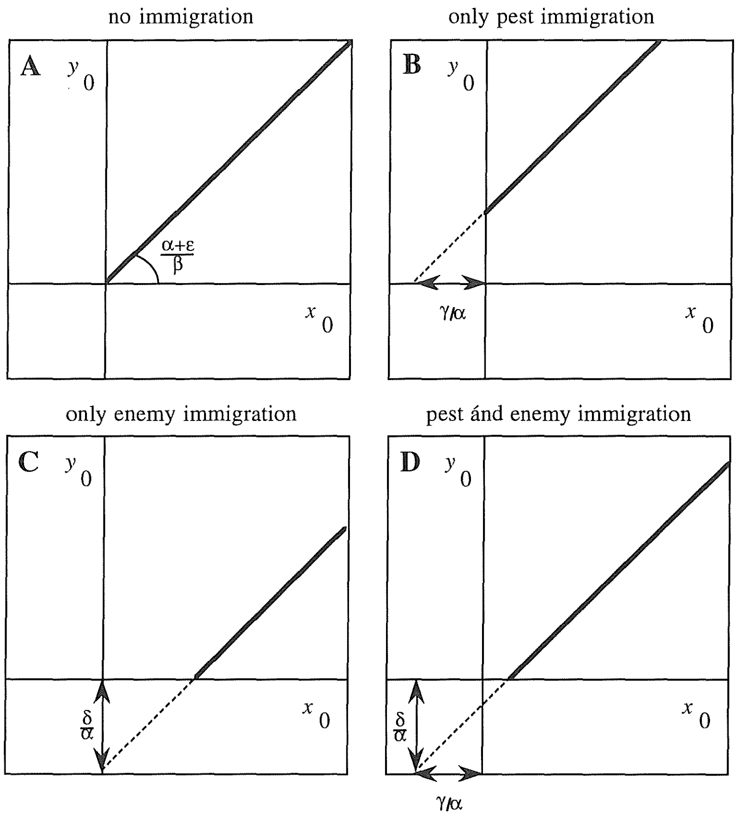


**Fig. 2.** The influence of immigration rates of a pest and its natural enemy on enemy/pest ratios required for preventing pest outbreak in Model 1. Meaning of symbols: $x_0$: initial pest density ([x]), $y_0$ : initial natural enemy density ([$y$]) $\alpha$: relative growth rate of pest ([$x$] [$x$]$^{-1}$ d$^{-1}$), $\beta$: feeding rate of natural enemy ([$x$] [$y$]$^{-1}$ d$^{-1}$), $\gamma$: immigration rate of pest ([$x$] d$^{-1}$), $\delta$: immigration rate of natural enemy ([$y$] d$^{-1}$), $\varepsilon$: relative emigration rate of natural enemy ([$y$] [$y$]$^{-1}$ d$^{-1}$). Bold drawn lines indicate initial densities of the enemy that are just sufficient for preventing pest outbreak at a given pest density. Figures A-D illustrate how this "critical" line is shifted by changing pest and enemy immigration rates. In figure A, immigration rates are 0. The bold line goes through the origin and has a slope of $(\alpha+\varepsilon)/\beta$. In figure B, the pest has non-zero immigration rate $\gamma$; this shifts the line to the left such that higher initial enemy densities are required. In figure C, the natural enemy has positive immigration rate $\delta$; this shifts the critical line downwards. Lower initial enemy densities give pest control. In figure D, both the pest and the enemy have positive immigration rates. The position of the critical line depends on the relative sizes of $\gamma$ and $\delta$, as well as on the slope of the critical line, $(\alpha+\varepsilon)/\beta$. The intercept of the critical line is defined by $\frac{\alpha+\varepsilon}{\beta}\,\frac{\gamma}{\alpha}-\frac{\delta}{\alpha}$.

term is a constant. The prey will be eradicated if the coefficient $A$ is negative. This leads to the following condition for biological control:

$$y_0 + \frac{\delta}{\alpha} > \frac{\alpha + \varepsilon}{\beta}\left(x_0 + \frac{\gamma}{\alpha}\right) \tag{4a}$$

Prey density will approach an equilibrium $x^* = -C$ if

$$y_0 + \frac{\delta}{\alpha} = \frac{\alpha + \varepsilon}{\beta}\left(x_0 + \frac{\gamma}{\alpha}\right) \tag{4b}$$

There will be a prey outbreak if

$$y_0 + \frac{\delta}{\alpha} < \frac{\alpha + \varepsilon}{\beta}\left(x_0 + \frac{\gamma}{\alpha}\right) \tag{4c}$$

Condition (4a) states that the predator/prey ratio should be greater than $(\alpha+\varepsilon)/\beta$ to prevent a pest outbreak when the pest and predator immigration rates ($\gamma$ and $\delta$) are 0 (Fig. 2A). The existence of this critical ratio was pointed out by Janssen & Sabelis (1992). When immigration rates are non-zero, the "critical" line, indicating for a given pest density the lowest predator density that will prevent an outbreak, is shifted along the axes (Fig. 2B-D). The slope of the line remains the same.

When $y_0 = y^*$, the time at which pest extinction takes place is:

$$\tau = \frac{1}{\alpha}\ln\left(\frac{C}{A}\right) \tag{5}$$

When $y_0 < y^*$, this is an underestimate of the time until extinction, else it is an overestimate. A precise estimate of $\tau$ can be obtained by simulation or iteration.

Fig. 3 explores the range of dynamics possible in Model 1. Fig. 3A shows how trajectories starting at initial densities ($x_0$, $y_0$) fulfilling (4a) converge to the equilibrium ($x^*$, $y^*$). Small deviations from the rule lead either to prey extinction or to a prey outbreak (Figs. 3B,C). Because of the sensitivity to initial conditions, the system is sensitive to timing. In Fig. 3D, simulations are shown in which the prey is given an advance on the predator of $\Delta t = 7$, 8, 9 or 10 days. During the predator-free period, the prey grows exponentially. When $\Delta t = 7$ days, the prey is eradicated after 8 days. When $\Delta t = 8$ days, eradication takes 23 days. When $\Delta t = 9$ or 10 days, there is a prey outbreak.

The integral of prey density over time provides a useful measure of the direct and indirect effects of aphids on crop growth and of vector pressure.

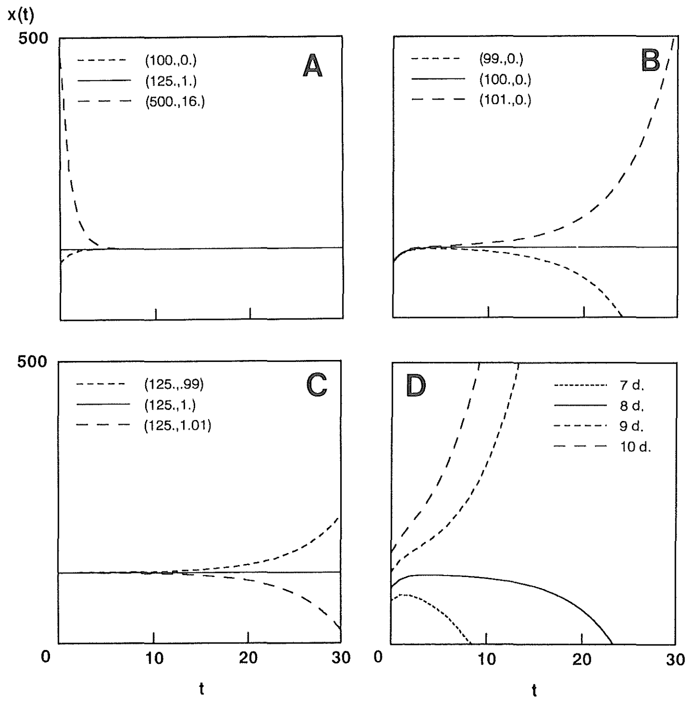


**Fig. 3.** Dynamics shown by Model 1 for parameter values $\alpha$ = 0.2 d$^{-1}$, $\beta$ = 30 aphids predator$^{-1}$ d$^{-1}$; $\gamma$ = 5 aphids m$^{-2}$ d$^{-1}$; $\delta$ = 1 ladybird m$^{-2}$ d$^{-1}$; $\varepsilon$ = 1.0 d$^{-1}$. A: convergence to equilibrium $x^*$ = $-C$ when condition 4b is fulfilled. B: divergence from equilibrium when prey density is 1% higher or lower than required by condition 4b. C: divergence from equilibrium when predator density is 1% higher or lower than required by condition 4b. D: Sensitive dependence of long term dynamics on the timing of predator immigration relative to that of the prey.

This integral (Area Under Curve) is:

$$\text{AUC} = \frac{A}{\alpha}\left(e^{\alpha t} - 1\right) + \frac{B}{\varepsilon}\left(e^{-\varepsilon t} - 1\right) - Ct \tag{6}$$

As in the threshold rule for biological control, all parameters and initial conditions have influence in this equation. Fig. 4 shows contour plots of log(AUC+1) over 30 days time in graphs of predator immigration rate, $\delta$,

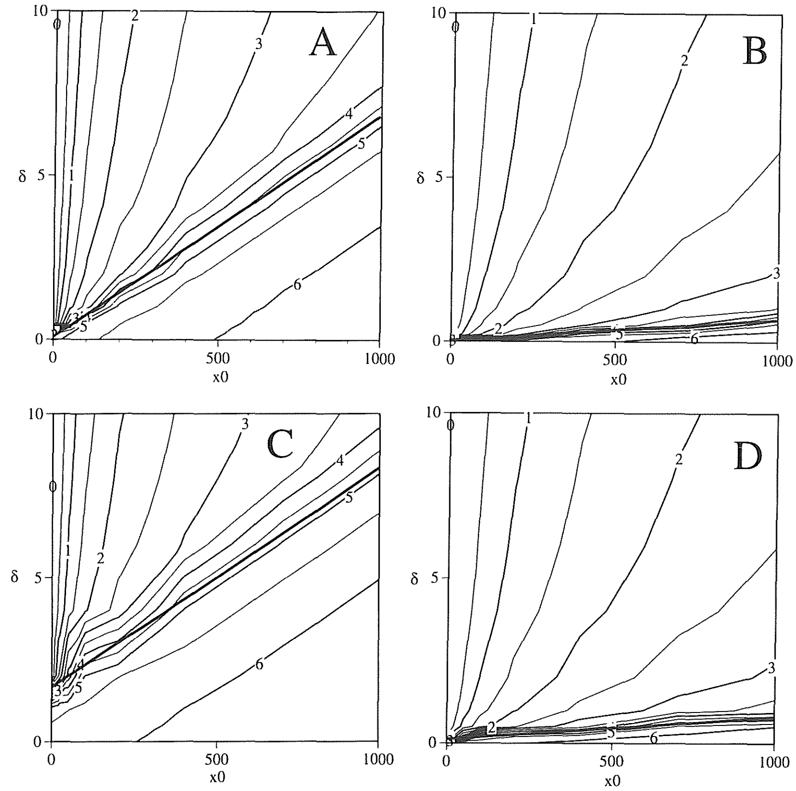


**Fig. 4.** Contour plots of log(AUC + 1) for four parameter settings in Model 1. The top and bottom two figures are characterized by *low* and *high* aphid immigration rates, respectively, while the left and right figures are characterized by *rapid* and *slow* predator departure. The parameter values are: (A) $\gamma$ = 5 [$x$] d$^{-1}$; $\varepsilon$ = 1 [$y$] [$y$]$^{-1}$ d$^{-1}$; (B) $\gamma$ = 5 [$x$] d$^{-1}$; $\varepsilon$ = 0.1 [$y$] [$y$]$^{-1}$ d$^{-1}$; (C) $\gamma$ = 50 [$x$] d$^{-1}$; $\varepsilon$ = 1 [$y$] [$y$]$^{-1}$ d$^{-1}$; (D) $\gamma$ = 50 [$x$] d$^{-1}$; $\varepsilon$ = 0.1 [$y$] [$y$]$^{-1}$ d$^{-1}$ . The values of the other parameters are: $\alpha$ = 0.2 d$^{-1}$; $\beta$ = 30 [$x$] [$y$]$^{-1}$ d$^{-1}$ and $y_0$ = $y$*. The thick drawn line in each of the figures is the critical line for eradication .

against $x_0$. Parameters are set to $\alpha = 0.2$ [x] [$x$]$^{-1}$ d$^{-1}$, $\beta = 30$ [$x$] [$y$]$^{-1}$ d$^{-1}$, $\gamma$ = 5 or 50 [$x$] d$^{-1}$, $\varepsilon = 1$ or 0.1 [$y$] [$y$]$^{-1}$ d$^{-1}$ and $y_0 = y^*$. In addition to the contour lines for log(AUC+1), a "critical" line is drawn in these figures that forms the distinction between combinations of $x_0$ and $\delta$ that do and do not result in ultimate aphid extinction. Below these "critical" lines, there is aphid outbreak, above them there is extinction. The critical lines are derived from Eqn 4. The intercept of these lines is $\gamma\epsilon/\beta$ while the slope is $\alpha\epsilon/\beta$. Comparison of the top and bottom figures illustrates the effect of *low* and *high* aphid immigration rates ($\gamma$) on the predator immigration rate required for biocontrol (defined in terms of extinction or AUC), as a function of initial aphid density. Comparison of the left and right figures illustrates the effect of *rapid* and *slow* predator departure ($\epsilon$). Predator departure is quite influential at all initial aphid densities; aphid immigration rate is only of substantial influence at low initial aphid densities. In all four figures, the critical line for eradication lies in the neighbourhood of the AUC contour for $10^4$ aphid days during 30 days. These results indicate that, by and large, predator immigration rates required for either definition of biological control (eradication or acceptable AUC) may be affected in a similar manner by model parameters. If tactical management is the objective, a criterion for biological control must be chosen. The criterion of final prey eradication has the advantage of being more simple to analyse in a model, but AUC as a criterion will often be more relevant from a practical viewpoint.

**Model 2. A prey-predator model with the predator feeding rate proportional to prey density**

In the first model, prey mortality due to predation is limited by predator feeding capacity, $\beta$. This allows the pest to escape eradication if the initial density is high enough. Such limited predation capacity may not be a fair description of reality. First, at low densities, prey finding is more limiting to the overall predation rate than is feeding capacity. Second, at high densities, coccinellids may kill more specimens than is required for meeting their food demand. The more prey are captured the less of each specimen is actually consumed (e.g. Kareiva & Odell 1987). Due to this "wasteful killing", the killing rate at high densities may not reach a plateau. In both situations, the killing rate is determined by the frequency of encounters between predator and prey. The relative death rate of prey is then proportional to prey and predator density:

$$\begin{cases} \dfrac{dx}{dt} = (\alpha - \kappa y)x + \gamma \\ \dfrac{dy}{dt} = \delta - \varepsilon y \end{cases} \qquad (7)$$

In the above equation, the effective relative growth rate of prey, $\alpha$-$\kappa y$, decreases linearly with $y$. The solution for prey equation (7) is:

$$x_t = \exp\left(-\frac{K}{\varepsilon}e^{-\varepsilon t} + r^* t\right)\left[x_0 \exp\left(\frac{K}{\varepsilon}\right) + \gamma\, F(t)\right] \qquad (8)$$

with

$$K = \kappa\left(\frac{\delta}{\varepsilon} - y_0\right) = \kappa(y^* - y_0)$$
$$r^* = \alpha - \kappa\frac{\delta}{\varepsilon} = \alpha - \kappa y^*$$
$$F(t) = \int_0^t \exp\left(\frac{K}{\varepsilon}e^{-\varepsilon t} - r^* t\right) dt \qquad (9)$$
$$y^* = \frac{\delta}{\varepsilon}$$

The predator equation is the same as before (cf. Eqn 2). The derived parameter $r^*$ is the relative growth rate of the prey in the long run. Equation (8) can be simplified making additional assumptions. For instance, in the absence of immigration of prey ($\gamma$=0), equation (8) simplifies to:

$$x_t = x_0 \exp\left(r^* t - \frac{K}{\varepsilon}(e^{-\varepsilon t} - 1)\right) \qquad (10)$$

When $t$ is several times greater than $1/\varepsilon$, equation (10) becomes approximately

$$x_t = x_0 \exp\left(\frac{K}{\varepsilon}\right) e^{-r^* t} \qquad (11)$$

Equation (11) denotes an exponential increase or decrease, depending on the sign of $r^*$.

For the assumptions $y_0 = y^*$ and $r^* \neq 0$, equation (8) simplifies to:

$$x_t = x_0 e^{r^* t} + \frac{\gamma}{r^*}(e^{r^* t} - 1) = \left(x_0 + \frac{\gamma}{r^*}\right)e^{r^* t} - \frac{\gamma}{r^*} \qquad (12)$$

When $r^*$ is greater than 0, this equation describes an exponential growth with relative rate of increase $r^*$. When $r^*$ is negative, Eqn 12 describes an exponential decline of prey density to a plateau level of $-\gamma/r^*$. When $r^*$ is equal to 0, prey population growth ultimately becomes linear with a rate equal to the rate of immigration, $\gamma$. Prey eradication proceeds as an exponential decline if there is no immigration. Fig. 5 gives examples of these types of dynamics.

For $y_0 = y^*$ and $r^* \neq 0$, cumulative prey density is given by

$$\text{AUC} = \frac{1}{r^*}\left(x_0 + \frac{\gamma}{r^*}\right)(e^{r^* t} - 1) - \frac{\gamma}{r^*}t \qquad (13)$$

Of the four unknowns in this equation, $r^*$ is by far the most influential one in the long run, when $r^* t >> 1$. Hence, in the second model, the components

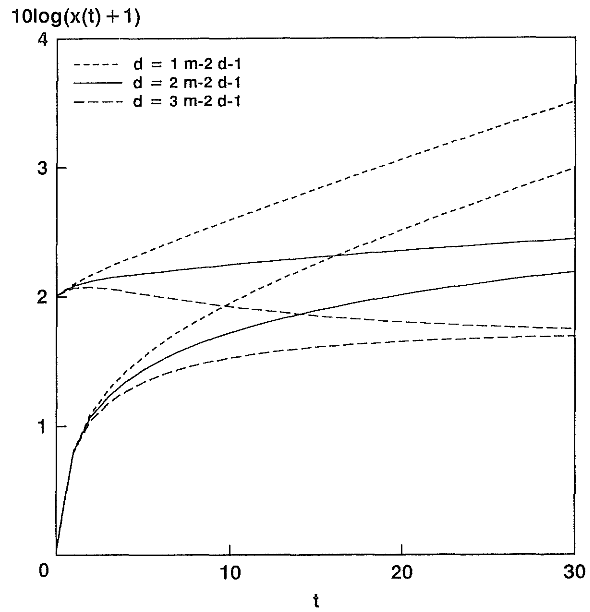


**Fig. 5.** Dynamics of Model 2 for parameter values $\alpha$ = 0.2 $d^{-1}$, $\kappa$ = 0.1 $d^{-1}$; $\gamma$ = 5 aphids $m^{-2}$ $d^{-1}$; $\varepsilon$ = 1.0 $d^{-1}$ and $\delta$ = 1, 2 or 3 ladybirds $m^{-2}$ $d^{-1}$ (i.e. $y^*$ = 0.1, 0 or -0.1 ladybirds $m^{-2}$ and $r^*$ = 0.1, 0 or -0.1 $d^{-1}$. The starting conditions are $(x_0, y_0)$ = (0, 0) and (100, 0).

of $r^*$ ($\alpha$, $\kappa$, $\delta$ and $\varepsilon$) have the biggest effect on AUC. Initial densities and prey immigration are of less importance.

## Experiments

Three experiments were done in the Netherlands in 1985 and 1986 to study the relationship between the date of primary virus infection with BYV and BMYV in sugar beet and the rate of virus spread by *M. persicae*. Details of these experiments are given by van der Werf et al. (1992). These experiments demonstrated substantial differences between fields in vector establishment and virus spread. In Experiments 1 and 2, aphid densities in the centre of artificially started virus foci stayed below 5 per plant while the final number of infected plants in a focus was c. 50. In Experiment 3, aphid densities reached a peak of c. 70 in early-inoculated and 35 in late-inoculated plots while the corresponding numbers of infected plants were c. 2000 and 100. Differences in virus spread between the three experiments were obviously related to the number of vectors. Differences in vector establishment were attributed to different impact of natural enemies, such as coccinellids, because reproduction of clipcaged aphids was

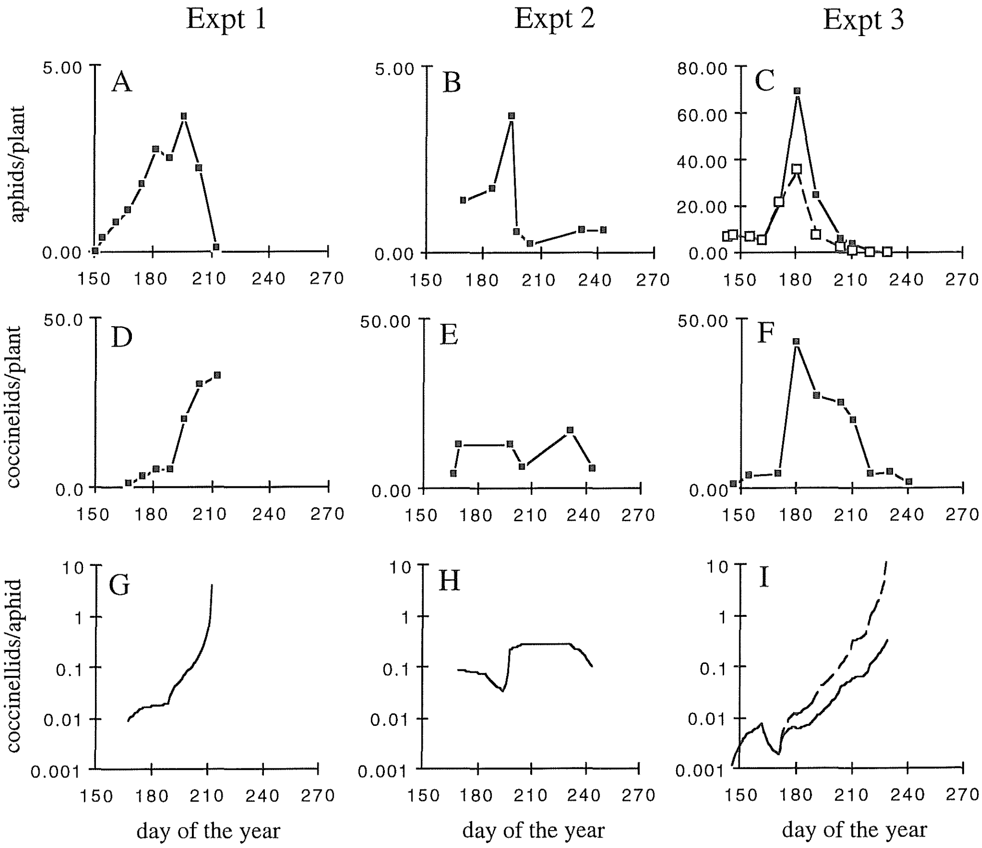


**Fig. 6.** Overview of aphid and coccinellid densities in three experiments on the spread of sugar beet yellowing viruses by the green peach aphid, *Myzus persicae*. The top row of graphs (A,B,C) indicates the time course of aphid density (*M. persicae* per plant; all stages lumped) in the three experiments. In Expt. 3, distinction is made between early-inoculated plots (inoculations until 10 June; —■—) and late-inoculated plots (inoculations after 20 June;- -□- -). The middle row of graphs (D,E,F) indicates coccinellid density (all species and stages lumped: an egg cluster counted as one). In Expt. 1, coccinellid density (individuals/plant) is derived from observed incidence (fraction occupied plants), assuming that the two are equal. The bottom row of graphs (G,H,I) indicates the ration of coccinellid to aphid density in the course of time. For Expt. 3, distinction is made between early inoculated plots (full line) and late inoculated plots (hatched line). Time is expressed in day of the year. The episodes marked by days 150, 180, 210, 240 and 270 broadly correspond to the months of June, July, August and September.

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There is an error in Fig. 6 on page 307. Density of coccinellids (D, E, F) is expressed per **100** plants.

found to be similar in the three fields. Observations on aphid density, coccinellid incidence and coccinellid/aphid ratio are summarized in Fig. 6.

If natural enemies were the main cause of the field to field differences in vector establishment and if coccinellids were — early on — (one of) the main predator group(s), then the information in Fig. 6 may give clues as to what criteria distinguish the initial predator-prey interaction in the three experiments, e.g. predator density, predator timing or a predator/prey ratio. The experimental results will first be interpreted in terms of Model 1, which led to a threshold rule that involved a predator/prey ratio with immigration terms $\left(\frac{\gamma}{\alpha} \text{ and } \frac{\delta}{\alpha}\right)$. The highest initial predator/prey ratio was observed in experiment 2. This ratio was well above a critical level for biological control of, say:

$$\frac{\alpha + \varepsilon}{\beta} = \frac{0.2 + 1.0}{30} = \frac{1}{25} \tag{14}$$

In estimating this critical ratio, prey and predator immigration are set to 0. In Experiment 1, the initial ratio was only 0.01, yet biological control occurred. Possibly, this discrepancy occurs because the assumption of zero immigration is unrealistic. If we take $y_0 = 0.01$, $x_0 = 1$ and $\gamma = 0$, then an immigration rate of only 0.006 coccinellid $m^{-2}\ d^{-1}$ would suffice to let the ratio rule (4) predict biocontrol. This low rate is easily achieved in practice (cf. Kareiva & Odell 1987). For lower emigration rates than 1 $d^{-1}$, lower rates of immigration would suffice for natural control. The importance of the predator immigration rate in Model 1 can be elucidated by assuming that the observed initial predator density is equal to the equilibrium density $y^*$. The threshold rule (4b) can then be written as:

$$y_0 + \frac{\varepsilon\, y_0}{\alpha} > \frac{\alpha + \varepsilon}{\beta}\left(x_0 + \frac{\gamma}{\alpha}\right) \tag{15}$$

If we assume an emigration rate of coccinellids $\varepsilon = 1\ d^{-1}$, then the immigration-dependent term $\varepsilon y_0/\alpha$ is five times greater than the density term $y_0$. For a lower emigration rate $\varepsilon = 0.1\ d^{-1}$, the immigration dependent term is smaller than $y_0$, but it is still of importance. Thus, if this model represents reality, immigration rate substantially modifies the predator-prey ratios predicting natural control. The lowest predator prey ratios were observed in Experiment 3. In the light of the outcomes of Model 1, it is not surprising that aphid population increase reached the highest peak densities in this experiment. The data in a broad sense support Model 1.

When Model 2 (with the feeding rate proportional to prey density) is considered applicable to the experiments, $r^*$ becomes the parameter of most interest. According to equation (9):

$$r^* = \alpha - \kappa y^* \tag{16}$$

If the initial density of coccinellids is assumed to be $y^*$, then, to explain the differences in vector establishment, this density should be higher in Experiments 1 and 2 than in Experiment 3, the other parameters, $\alpha$ and $\kappa$, being equal. Experiment 2 has indeed the highest initial coccinellid density, but Experiments 1 and 3 show different aphid population trends in spite of similar coccinellid densities. The disaccordance can be used to reject the model or to expand the hypothesis. In Experiment 3 (with BYV) *M. persicae* reproduction may have been enhanced by the effects of this virus on host plant quality (Baker 1960), while in Experiment 1 (with BMYV for which such an effect has not been described) this might not have occurred. Another explanation for the lower *M. persicae* densities in Experiment 1 may be that in this experiment there was a substantial population of *A. fabae*. The availability of alternative prey may have decreased the emigration rate of coccinellids.

## Discussion

The models provide a framework to interpret the field experiments, but too many parameters are unknown in the experiments to reject any of the models. The models are also too abstract to warrant formal rejection because they can only represent main features of the system and not the smaller details (as virus-enhanced reproduction) that are important in reality but that would hamper a lucid theoretical analysis.

The theoretical analysis of the (admittedly too) simple models yields some interesting results. In both models a critical criterion can be derived that distinguishes situations that will result in an exponential prey outbreak from cases in which the prey will be eradicated (Model 1) or kept at a constant level (Model 2). In Model 1, where predator feeding rate is a constant, this threshold rule weights predator density, immigration and emigration against prey density, population growth and immigration. Initial densities are important here, as are immigration rates, relative growth or emigration rates and predator feeding rate. In the second model, where predator feeding is proportional to prey density, initial densities are not important. Here prey relative growth rate compared to predator equilibrium density and searching capacity determine the occurrence of outbreaks. The first model shows a threshold behaviour in which the prey can escape from predation and cause an outbreak if it establishes populations early enough. Timing is crucial in this model. In Model 2, predators can always catch up with a prey advance because their per capita feeding rate is unlimited. Model 1 seems to be more in accordance with reality than Model 2. The threshold rule (Eqn 4) may prove useful for estimating the beneficial effect of natural enemies immigrating from nearby reservoirs.

It is important to relate immigration rates to landscape because landscape may be managed such that biological control is favoured and dependence on pesticides reduced. The fields where *Myzus* population buildup was prevented and hence virus spread limited, were situated south of Wageningen, in an environment with hedgerows and overwintering hosts of black bean aphid, *Aphis fabae*. The vicinity of hedgerows and the early infestation of the sugar beet crop with *Aphis fabae* could cause a greater and/or earlier settlement and impact of natural enemies in the experiments done here. The experiment with the greater amount of spread was laid out in the open landscape of the polder Oostelijk Flevoland, which presumably provides fewer overwintering sites for coccinellids.

To substantiate the beneficial effect of natural enemy winter reservoirs in agroecosystems, quantitative insight will be needed in immigration rates of natural enemies in relation to distance between source and destination. The emphasis should be on quantifying process parameters, not on registering anecdotal information such as maximum possible dispersal distances. More important are the processes underlying spatio-temporal (re)distribution of natural enemies in the early growing season when pests and diseases are about to take either an outbreak or an extinction course. Studies on local dynamics of pests and diseases need to be supplemented with measurements of immigration. To be useful for biological control analysis, studies on spatial dynamics of natural enemies need to be carried out with a fine time resolution in the early growing season because the early system dynamics may be quite sensitive to timing. This is currently not always done. For instance, Basedow (1990) reported differences in natural enemy catches during two month periods in arable fields in different landscapes. To estimate the importance of these differences for pest dynamics it is necessary to know when these differences occurred. It is to be expected that a small difference in the density of natural mortality agents in May is much more important for the dynamics of pest and diseases than a much greater difference in July. Another point that deserves continued and wider attention is the scaling up of functional responses from the level of the petri dish to the level of the crop. One way to do this is to make explicitly spatial models (Kareiva & Odell 1987). This is, however, no practical way ahead for models to be used in tactical management. For such purposes, simulation and experimentation approaches towards deriving descriptive equations for functional responses at greater spatial scales (van der Werf et al. 1989, Mols 1993) are more promising.

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SPATIAL HETEROGENEITY



DISCUSSION PAPER



DISPERSAL

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**Density, spatial heterogeneity and dispersal**

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