

Sampling predator/prey ratios to predict cumulative pest density in the mite - predatory mite system *Panonychus ulmi* - *Typhlodromus pyri* in apples

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SUMMARY

Predator/prey ratios have been advocated as sampling statistics that are indicative of biological control. Dynamic population models can be used to explore the relationship between such ratios and cumulative pest density, as a measure for pest population development and damage. Two types of models can be used: simulation models incorporating much biological detail and simplified theoretical models. We analysed results of simulations with both types of models by plotting contours of cumulative pest density in graphs with initial pest and predator density on the axes. In such graphs, straight lines through the origin represent constant initial predator/prey ratios. Predator/prey ratios would be good predictors of cumulative pest density if the contours conformed closely to such straight lines through the origin. This was not the case in either model. Nevertheless, calculations with the simulation model for 10 years weather data indicated that a predator/prey ratio of 1:10 would almost always yield biological control. This was true for situations with and without alternative food for the predator. Although the minimum (critical) predator densities required for biological control are not precisely a multiple of initial pest mite density, a predator/prey ratio still provides a usable approximate criterion for assessing the likelihood of biological control. Simulations with simple models in a qualitative sense confirmed trends observed with the simulation model.

INTRODUCTION

When biological control relies on naturally occurring enemies of pests, sampling information and a decision criterion based on the sampling information is needed to assess the

likelihood of biological control. A ratio of natural enemy density to pest density (or vice-versa) may be a suitable decision criterion. Such a ratio quantifies the common-sense notion that a pest density that is twice as high requires twice as many predators to be controlled. Predator/prey ratios may also be used to calculate the number of natural enemies that need to be released when predators or parasitoids are applied as a 'biological pesticide'.

The use of predator/prey ratios for predicting biocontrol was introduced 20 years ago by Croft (1975a,b), who worked on integrated management systems for fruit tree red spider mite *Panonychus ulmi* in apples. This mite can be controlled by naturally occurring predatory mites from the family Phytoseiidae: *Typhlodromus pyri*, *Amblyseius fallacis*, *A. potentillae* and *Metaseiulus occidentalis*, but biocontrol is easily disrupted by broad-spectrum pesticides. Sampling is required to make sure that biocontrol is effective. Croft considered the ratio of the density of the predator *Amblyseius fallacis* to the density of *P. ulmi* when the density of the latter was greater than seven per leaf. For lower pest density no action was considered necessary. Based upon the ratio, he classified the situations with high red mite density into six categories, characterized by the estimated likelihood of biocontrol and the advised management action. Although the scientific basis for Crofts scheme was not made explicit, his approach was a breakthrough in mite management thinking.

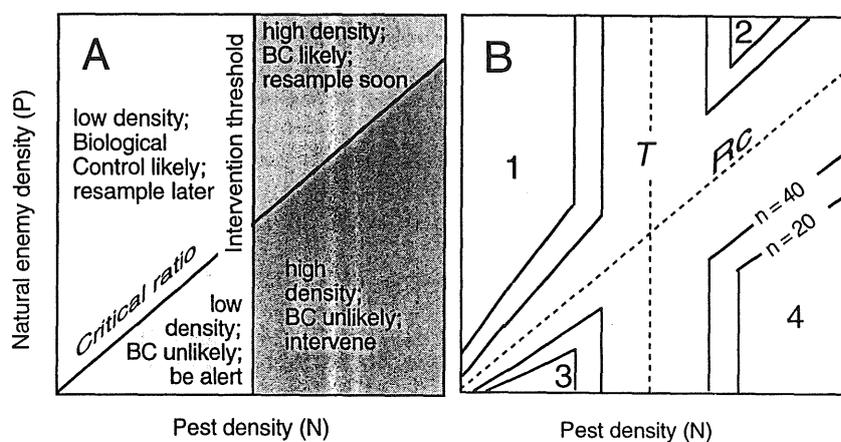


Fig. 1: Protocol for simultaneous classification of pest & predator density with respect to an intervention threshold T for the pest and with respect to a critical ratio R_c for the pest/enemy density ratio (after Nyrop, 1988)

Nyrop (1988) embedded Crofts approach in a formal sampling framework, considering only two situations: biocontrol likely or unlikely. His scheme is based upon classification of spider mite density with reference to an intervention threshold, T (10 mites per leaf), and simultaneous classification of the prey/predator ratio, R , with reference to a critical ratio of 5 red mites per predator. (The predator species is here *Typhlodromus pyri*.) There are four different classifications in this scheme (Fig. 1A). The sampling procedure works as follows. A random

sample of $n = 20$ leaves is taken in the orchard and the mean density of pest, N , and predator mites, P , is determined. The outcome of the sample in the form of the point (N, P) is plotted in Fig. 1B and compared to the stoplines for $n = 20$. If the point is within the cross formed by the vertical stoplines for pest density and the slanted (curved) stoplines for the pest/predator ratio, the conclusion is that the sample information is close to (i.e. not significantly different from) the intervention threshold, the critical ratio or both. A new sample of 20 leaves is then taken, and the resulting point is again compared to the stoplines for $n = 40$. When the points falls outside the cross formed by the stoplines for that sample size, a classification of the population into one of the regions 1-4 is made and the corresponding management decision is taken. The procedure is repeated until a decision is taken or until 100 leaves have been inspected. When the maximum sample size is reached without a decision, the point is classified by comparison with the intervention threshold T and the critical ratio R_c .

The position of the stoplines is calculated by constructing confidence intervals around the intervention threshold and the critical ratio, under the assumption that the sample means for pest and predator density are correlated normal random variables. In ratio-based management schemes like those described by Croft (1975a,b), Hoy (1985) and Nyrop (1988), the existence is assumed of a well-defined critical ratio that distinguishes situations that result in biological control from those that do not.

Work has been done to validate this assumption, with the emphasis on modelling because it is laborious and costly to do this in field experiments. Some authors have used simulation models that describe population processes to a high degree of detail, including aspects of temperature-dependent phenology, survival, age-dependent reproduction, stage-dependent predation, etc. Coworkers of Croft (Dover *et al.*, 1979) used a simulation model to investigate the relationship between initial pest and predator (*A. fallacis*) densities and the peak density achieved by *P. ulmi*. Their results were inconclusive. Using a detailed simulation model of the interaction between *A. potentillae* and *P. ulmi*, Rabbinge (1976) found that predator/prey ratios as low as 1/10 in mid-May were sufficient to keep seasonal peak densities of *P. ulmi* below a level of three per leaf (which was considered a damaging density), whereas lower ratios of 1/100 were not adequate. Other authors used caricatural mathematical models that represent only major features of a predator-prey system, to investigate the relationship between predator/prey ratios and biological control. Janssen & Sabelis (1992) used an extremely simplified predator-prey model to assess how the relative rates of increase of pest and predator and the feeding rate of the predator affected the range of predator/prey ratios resulting in ultimate pest eradication. In their very simplified model, the initial predator/prey ratio was a sufficient predictor of ultimate pest eradication. Besides pest eradication, they considered the integral of pest density until the moment of extinction (AUC: Area Under the Curve). This integral is an indicator for damage by mites (e.g. Hardman *et al.*, 1985) and many other pests and diseases. The initial predator/prey ratio was not a sufficient predictor of the integral of pest density up to the time of eradication (see Appendix).

While Janssen & Sabelis' analysis shows that predator/prey ratios are in theory not perfect predictors of AUC, it may still turn out that the relationship between the initial predator/prey ratio and the AUC is good enough to be practically usable. In this paper we use a simulation model to explore the range of critical ratios for the *P. ulmi* - *T. pyri* system, as influenced by weather conditions and the presence of alternative food for the predator. These are

two major factors known to influence biological control success. We use simple models to investigate how the presence of alternative food and predator cannibalism might affect the relationship between predator/prey ratios and AUC.

MATERIALS AND METHODS

Simulation runs with the detailed and simple models were conducted for matrices of initial densities of the prey and the predator. By doing hundreds of simulations, starting at different points in the initial state plane, it is possible to divide this plane into regions that produce different integrals of prey density over time (AUC). Initial ratios of predator to pest density are represented by lines in the plane that have a slope equal to the ratio (or with some authors, e.g. Nyrop (1988), the reciprocal of the ratio). A visual inspection of the shape of the contours produced by connecting points with equal (interpolated) AUC indicates how useful ratios are for predicting biological control.

Simulation model

The simulation model describes development, survival and reproduction of *P. ulmi* and *T. pyri* under the influence of environmental factors (temperature, rainfall, daylength), host plant age and the effects of the two populations on each other. Details of structure, parameters and validation of the model are given by Hardman (1989) and by Walde *et al.* (1992). To produce each contour plot of cumulative mite density, 400 simulations were done for a 20 x 20 matrix of initial densities of the prey (0-10 mites/leaf) and the predator (0-1 mites/leaf). These simulations were done for 10 years of weather data, recorded in Geneva NY, and with or without alternative food for the predator. Alternative food is an important factor contributing to persistence and biocontrol efficacy of *T. pyri* (Walde *et al.*, 1992).

Simple models

Simple models are based on logistic growth of pest mite density, N , with rate of increase r , maximum K , and a death rate proportional to the density of the predator, P . The feeding rate of the individual predator is a saturating function, $f(N)$, of mite density. The predator has a death rate d in the absence of prey while predator reproduction is proportional to the number of prey consumed: $c f(N) P$. The model is simulated by rectangular integration with a time step of one day. Densities are expressed per leaf.

$$1. \begin{cases} \frac{dN}{dt} = r \left(1 - \frac{N}{K}\right) N - f(N) P \\ \frac{dP}{dt} = c f(N) P - d P \end{cases}$$

Parameter values appropriate for the *P. ulmi* - *T. pyri* system are:

$$r = 0.15 \text{ day}^{-1}; K = 50 \text{ mites per leaf}; c = 0.05 \text{ predators per prey}; d = 0.1 \text{ day}^{-1}$$

The functional response, $f(N)$ is: $f(N) = F (1 - 2^{-N/H})$, where F is the maximum *per*

capita feeding rate of the predator and H the prey density at which feeding rate is 50% of the maximum. $F = 4$ mites predator⁻¹ day⁻¹; $H = 4$ mites per leaf. Parameter values are only indicative and will in reality vary substantially in time, with circumstances and from field to field. Two extended models take into account alternative food (A) (model 2) and cannibalism (model 3).

$$\begin{array}{l}
 2. \quad \begin{cases} \frac{dN}{dt} = r \left(1 - \frac{N}{K}\right) N - f(N, A) P & f(N, A) = \frac{N}{N+A} F \left(1 - 2^{-(N+A)/H}\right) \\ \frac{dP}{dt} = c f(N, A) P + c g(N, A) P - d P & g(N, A) = \frac{A}{N+A} F \left(1 - 2^{-(N+A)/H}\right) \end{cases} \\
 3. \quad \begin{cases} \frac{dN}{dt} = r \left(1 - \frac{N}{K}\right) N - f(N, P) P & f(N, P) = \frac{N}{N+0.2P} F \left(1 - 2^{-(N+0.2P)/H}\right) \\ \frac{dP}{dt} = c f(N, P) P - (1-c) g(N, P) P - d P & g(N, P) = \frac{0.2P}{N+0.2P} F \left(1 - 2^{-(N+0.2P)/H}\right) \end{cases}
 \end{array}$$

In model 2, it is assumed that there is 'free competition' among the predator food items 'prey' and 'alternative food', such as other mite species, pollen, etc. The assumption of free competition implies non-preference for food items of the predator, which is almost certainly an oversimplification, but warranted in view of the incomplete understanding of food selection by *T. pyri* (Dicke *et al.*, 1989) and the methodological difficulty of quantifying pollen as an important alternative food item. A is set at a moderate level equal to H . In model 3, it is assumed that the proportion of encounters with predator victims resulting in feeding is one fifth of that for prey victims, while the food content and quality of predator victims is the same as that of *P. ulmi*. This description is supported by laboratory observations (J.P. Nyrop; unpublished results).

The simulations were programmed in Mathematica 2.0 (Wolfram, 1991) and done on a Macintosh Quadra 650 personal computer. Mathematica notebooks are available on request.

RESULTS

Simulation model

The simulation model of the *P. ulmi* - *T. pyri* system was used to identify initial states of the system that would result in biocontrol, defined as $AUC < 750$ mite-days. The model was run for New York weather data 1981 - 1991 and for two different alternative food levels; none and low. The low level corresponds to 25% of *T. pyri* food demand before 1 July and 5% afterwards. Fig. 2 shows the results for two extreme years: the warm and dry year of 1983 (cumulative rainfall 10 June - 15 September of 161 mm and a temperature sum >7 °C of 2100 °C day) and the cool and wet year of 1984 (cumulative rainfall 10 June - 15 September of 364 mm and a temperature sum >7 °C of 1930 °C day). The comparison between years shows that the low mortality of *P. ulmi* caused by the dry weather in 1983 results in high densities of *T. pyri* being needed for biological control. When alternative food is present, performance of *T. pyri* is substantially improved. Hence, lower initial densities of the predator give biological control. All the figures show distinct signs of nonlinearity, in the sense of deviations from the expected

monotonic decrease of AUC with increasing predator density for a given prey density or the expected monotonic increase of AUC with increasing pest density at given predator density. For instance: in 1983 with no alternative food and an initial density of 3.2 *P. ulmi* per leaf, an AUC of 1750 mite-days per leaf results from initial *T. pyri* densities that are low (0.03) or medium high (0.20) while at intermediate densities of about 0.10 *T. pyri* per leaf the AUC is only about 1250 mite-days. Such lower AUCs also result from quite high initial *T. pyri* densities of more than 0.25 per leaf. The reason for the fairly high AUC with initial *T. pyri* densities of around 0.20 mites per leaf is that these densities provide sufficient mortality in the first two generations of red mite to allow a third generation. With somewhat lower initial *T. pyri*

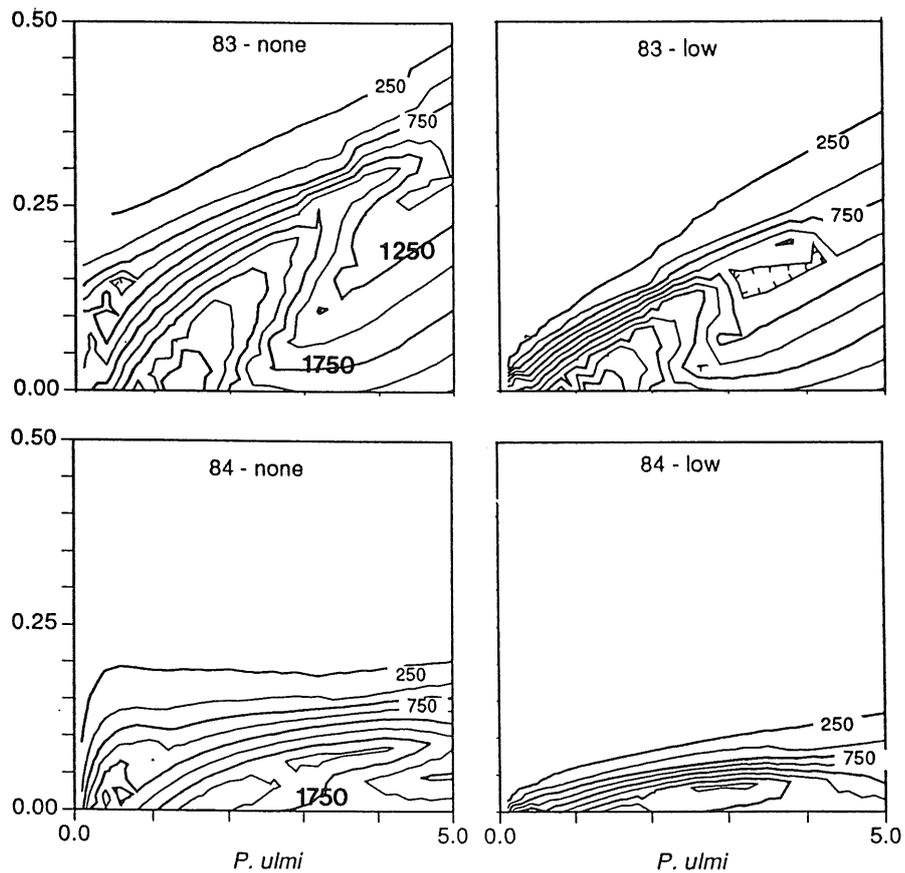


Fig. 2: Contour representation of the response surface $AUC = h(N_0, P_0)$ for the simulation model with no or a low level of alternative food for an extremely dry year (1983) and an extremely wet year (1984). Simulations were started on 10 June (day 161) with *P. ulmi* and *T. pyri* initialized as adults. Simulations were halted on 15 September (day 258).

densities, the first two generations are greater, causing such leaf damage early on that winter eggs are produced instead of an extra generation. The overall AUC is then smaller. These nonlinear phenomena conflict with the idea of the predator/prey ratio predicting AUC.

The simulation model also produces non-linear effects with respect to temperature (results not shown). Here the nonlinearity is due to the fact that in the model, the *P. ulmi* population is initially strongly synchronized. When temperature, that drives phenology, puts a substantial part of the population in rain-susceptible motile stages when rain showers occur, mortality will be high and biocontrol will be attainable with few *T. pyri*. When temperature is either higher or lower, mortality will be lower, such that more *T. pyri* are needed for biocontrol.

Simple models

Dynamics of the standard model is presented in Fig. 3A. The system shows outward spiralling dynamics around a steady state (N^* , P^*), which is defined by the intersection of the zero growth isoclines of the predator and the prey. Figs 3B-D present the AUC for prediction periods of 7, 15 and 30 days.

When the prediction period is short the contours are still comparable to straight lines through the origin, indicating that then the initial ratio gives a usable prediction of the area under the curve (AUC). But non-linear effects become more apparent as the length of the prediction period increases (Fig. 3D). The figures show that the change of predicted AUC per unit change of N_0 , P_0 or ratio is very different in different parts of the plane for the longer prediction periods. For instance, in the upper part of Fig. 3D, with high P_0 values, the effect of a change in the value of N_0 or P_0 on AUC is small, as indicated by the large distance between contour lines, which in this part of the plane delimit areas with low AUCs. In the lower part of the plane, with small P_0 values, the predicted AUC is sensitive to changes in P_0 , as indicated by the closeness of contour lines that here separate areas with substantially different AUCs. Except for the area close to the origin, the AUC is insensitive to changes in N_0 in the bottom part of the initial state plane; the contours are horizontal. This indicates that not the ratio but the absolute value of P_0 is important here. Close to the origin, the AUC is very sensitive to both N_0 and P_0 .

Some contours remain in the same place from short to long prediction intervals. Compare for instance the contours for AUCs 1, 2, 5 and 10 in the top half of the figures 3B-D. The reason for the similarity is that for these starting values, the system quickly settles in the area of slow dynamics at low densities near the ordinate and the origin. Here few mite-days are accumulated, and biocontrol is attained. The same phenomenon can occur if a trajectory spirals closely around a steady state with a low value of N^* .

The question whether the initial ratio is a usable predictor of biocontrol can be answered positively for the shorter prediction periods and the lower AUCs. Then the true contours can be approximated by straight lines through the origin. Ratios are not without qualification appropriate for the longer prediction period of 30 days. This limitation may be somewhat alleviated by considering only ratios for $N_0 > 2$.

Fig. 3 shows dynamics and AUC for the models 2 (+ alternative food) and 3 (+ cannibalism). Due to the presence of alternative food, the predator isocline in Fig. 4A is shifted to the left. With the parameters chosen here, the relative rate of increase of predators is at least

zero. As pest population growth is bounded by the maximum density K , the system ultimately results in pest extinction. Alternative food lowers initial predator densities needed for biocontrol at given initial pest density and the AUC contours are more similar to straight lines through the origin than with model 1 (compare Figs 3D and 4C). Hence the tentative conclusion can be drawn that the initial predator prey ratio is a better predictor in the system with alternative food than in the original system without alternative food. Cannibalism has the opposite effect. The predator isocline is slanted to the right, indicating higher prey density is needed to support predators when the latter are cannibalistic. As a consequence, higher P_0 is needed for biocontrol than in the standard model.

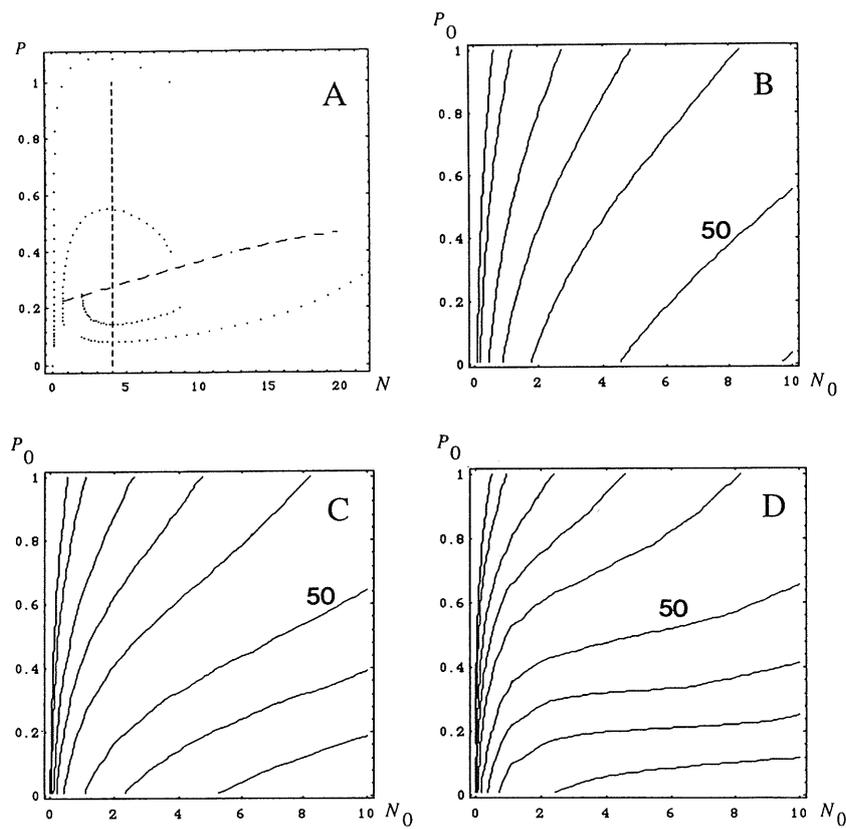


Fig. 3: Dynamics and AUC of the simple model 1, without cannibalism or alternative food. A: Zero growth isoclines of prey (---) and predator (.....) and four dynamic trajectories during 30 days. Trajectories start at the points (2, 0.1), (2, 0.25), (8, 0.4) and (8, 1). B, C & D: Contour plots of cumulative mite density over 7, 15 and 30 days, respectively. AUC contours form an exponential series from top left hand to bottom right: 1, 2, 5, 10, 20, 50, 100, 200, 500.

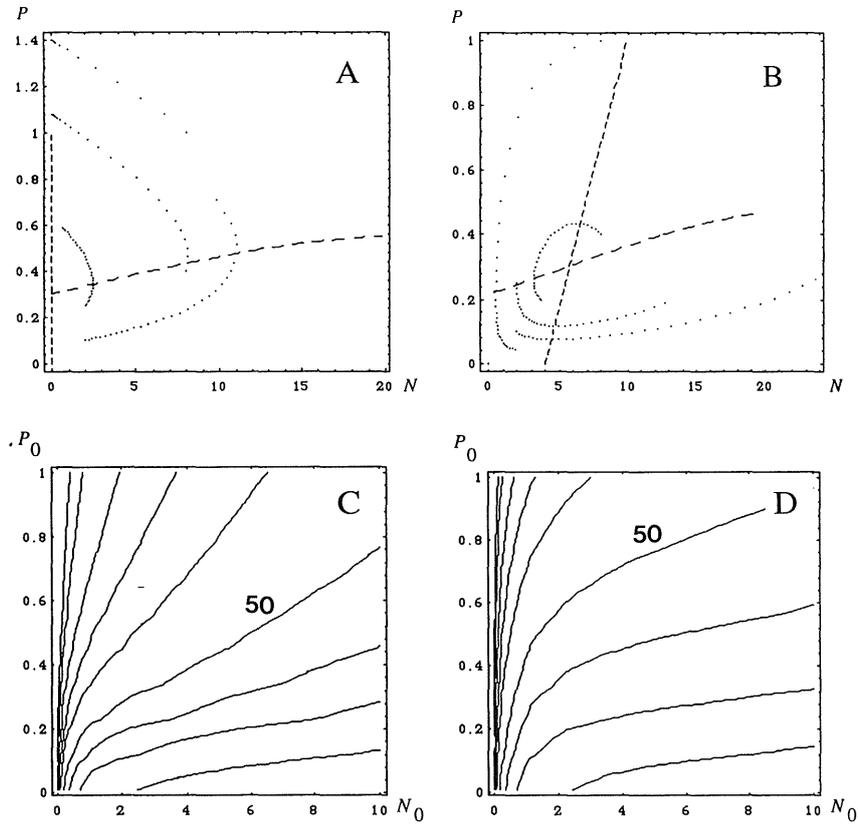


Fig. 4: Dynamics (A, B) and AUC over 30 days (C, D) of the simple models 2 (+ alternative food: A, C) and 3 (+ cannibalism: B, D). Initial states and contours as in Fig. 3.

Besides similarities, there are also substantial differences between AUC plots in the initial state plane, produced by simple models and those produced by the simulation model. For instance, in all the figures based on simple models, the AUC is relatively insensitive to N_0 for low values of P_0 . This is in contrast to the plots based on the simulation model.

DISCUSSION

Results obtained with the simulation model confirm the assertion of several researchers that a ratio of more than 1 predatory mite per 10 spider mites predicts biocontrol. A ratio of 1 to 10 gave simulated biocontrol of *P. ulmi* by *T. pyri* even in the worst year out of 10, in which warm dry weather favoured an outbreak of *P. ulmi*. In years less favourable for *P. ulmi* the

simulation model calculates biological control for ratios as low as 1:50. The simulation model clearly demonstrates the importance of weather and alternative food for the predator for successful biocontrol. The latter conclusion was confirmed with the simple models. Both types of model show marked nonlinear effects close to the origin and for high AUCs, resulting from low P_0 . The simple models in addition show high sensitivity of AUC to P_0 when P_0 is low, but this was not confirmed by the simulation model. Nonlinear effects and high sensitivity to initial conditions limit the usefulness of an initial predator/prey ratio as a predictor of AUC, but the fact that these problems occur especially for low P_0 is fortunate because from a sampling perspective it is laborious to make precise population estimates at low densities.

The overall conclusion that emerges is that predator/prey ratios may be usable predictors of predator/prey system dynamics, AUC and biological control, even if from a theoretical perspective, they cannot be exact. It is however questionable whether it is practical to estimate predator/prey ratios. Estimating natural enemy complexes may increase labour beyond what is necessary. A useful alternative to observing natural enemy density is to monitor the population trajectory of a pest species through time (Nyrop & van der Werf, 1994). The presence of predators will then manifest itself by their effect on the dynamics of the prey. In such monitoring schemes information about predator density or predator/prey ratios may be used to modify predictions of pest growth rates and hence optimize the scheduling of future sampling.

REFERENCES

- Croft, B.A. (1975a). *Integrated control of apple mites*. Extension Bulletin E-825, Cooperative Extension Service, Michigan State University, 12 pp.
- Croft, B.A. (1975b). Tree fruit pest management. In: R.L. Metcalf & W.H. Luckmann (Eds): *Introduction to insect pest management*. Wiley, New York, p. 471-507.
- Dicke, M., M.W. Sabelis & H. van den Berg (1989). Does prey preference change as a result of prey species being presented together? Analysis of prey selection by the predatory mite *Typhlodromus pyri* (Acarina: Phytoseiidae). *Oecologia* **81**, 302-309.
- Dover, M.J., B.A. Croft, S.M. Welch & R.L. Tummala (1979). Biological control of *Panonychus ulmi* (Acarina: Tetranychidae) by *Amblyseius fallacis* (Acarina: Phytoseiidae) on apple: a prey-predator model. *Environmental Entomology* **8**, 282-292.
- Hardman, J.M. (1989). Model simulating the use of miticides to control European red mite (Acarina: Tetranychidae) in Nova Scotia apple orchards. *Journal of Economic Entomology* **82**, 1411-1422.
- Hardman, J.M., H.J. Herbert, K.H. Sanford & D. Hamilton (1985). Effect of populations of the European red mite, *Panonychus ulmi*, on the apple variety Red delicious in Nova Scotia. *Canadian Entomologist* **117**, 1257-1265.
- Hoy, M.A. (1985). Integrated mite management for California almond orchards. In: W. Helle & M. Sabelis (Eds): *Spider mites, their biology, natural enemies and control*. World Crop Pests, Volume 1B, Elsevier, Amsterdam, p. 299-310.
- Janssen, A. & M.W. Sabelis (1992). Phytoseiid life-histories, local predator-prey dynamics, and strategies for control of tetranychid mites. *Experimental & Applied Acarology* **14**, 233-250.
- Nyrop, J.P. (1988). Sequential classification of prey/predator ratios with application to

- European red mite (Acari: Tetranychidae) and *Typhlodromus pyri* (Acari: Phytoseiidae) in New York apple orchards. *Journal of Economic Entomology* **81**, 14-21.
- Nyrop, J.P. & W. van der Werf (1994). Tripartite classification and adaptive frequency classification sampling plans for monitoring population density through time. *Aspects of Applied Biology* **37**.
- Rabbinge, R. (1976). *Biological control of fruit-tree red spider mite*. Pudoc, Wageningen, Netherlands, 228 pp.
- Walde, S.J., J.P. Nyrop & J.M. Hardman (1992). Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Experimental and Applied Acarology* **14**, 261-291.
- Wolfram, S. (1991). *Mathematica, a system for doing mathematics by computer*. Addison-Wesley Publishing Company, Redwood City, California, 992 pp.

APPENDIX

Janssen & Sabelis (1992) analysed the model

$$\begin{cases} \frac{dN}{dt} = \alpha N - \beta P \\ \frac{dP}{dt} = \gamma P \end{cases}$$

where α is the relative growth rate of the pest, β the per capita feeding rate of the predator and γ the relative rate of increase of the predator. It is easily derived that the prey will always be eradicated if the predator increases more rapidly than the prey ($\gamma > \alpha$). If $\gamma < \alpha$, eradication occurs if the initial predator/prey ratio exceeds a critical value:

$$R_c = \frac{\alpha - \gamma}{\beta}$$

The time at which eradication takes place is a logarithmic function of the initial predator/prey ratio:

$$\tau = -\frac{1}{\alpha - \gamma} \ln\left(1 - \frac{\alpha - \gamma}{\beta} \frac{N_0}{P_0}\right) = -\frac{1}{\alpha - \gamma} \ln\left(1 - \frac{R_c}{R_0}\right)$$

where R_0 and R_c are the initial and critical predator/prey ratios, respectively. The cumulated pest density until the moment of eradication is:

$$AUC = \frac{1}{\alpha} N_0 (e^{\alpha\tau} - 1) - \frac{\beta}{\alpha - \gamma} P_0 \left[\frac{1}{\alpha} (e^{\alpha\tau} - 1) - \frac{1}{\gamma} (e^{\gamma\tau} - 1) \right]$$

The occurrence of eradication and the timing of it are functions of the initial predator/prey ratio alone, whereas the cumulative pest density until extinction is also proportional to the absolute sizes of N_0 and P_0 . This can be shown by writing the last equation in the form:

$$AUC = N_0 \left[\left(1 - \frac{R_0}{R_c}\right) \frac{1}{\alpha} (e^{\alpha\tau} - 1) + \frac{R_0}{R_c} \frac{1}{\gamma} (e^{\gamma\tau} - 1) \right]$$

The initial ratio determines the shape of the pest population curve, while the absolute sizes of N_0 and P_0 determine the level. In this model, which is one of the simplest conceivable, the initial predator/prey ratio is therefore not a sufficient statistic for predicting AUC.