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Phytoseiid life-histories, local predator–prey dynamics, and strategies for control of tetranychid mites

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ABSTRACT

Janssen, A. and Sabelis, M.W., 1992. Phytoseiid life-histories, local predator–prey dynamics, and strategies for control of tetranychid mites. *Exp. Appl. Acarol.*, 14: 233–250.

Numerous studies have been devoted to estimating the intrinsic rates of increase, r_m , of phytoseiid and tetranychid mites. Intrinsic rates of increase may be helpful for biological control purposes, but how exactly is still unclear. In this paper, we show how r_m s can be used to this end, by using a simple model for the local dynamics of predator and prey populations. The application of this model critically depends on what is meant by the term local. Here, we define it as a spatial scale at which predator and prey dynamics are strongly coupled.

Furthermore, it is shown that the r_m of phytoseiid and tetranychid mites are correlated with mean and peak oviposition rates. Since peak oviposition rates are easy to determine, the regression equation provides a quick and simple way to estimate r_m . Subsequently, it is possible to calculate appropriate predator/prey ratios for biological control by using the model and the estimated r_m .

INTRODUCTION

Tetranychid mites are known as important pests of various crops (Helle and Sabelis, 1985a,b). Although the amount of damage inflicted by individual mites is low, their high rates of increase cause a rapid build-up of populations once a plant is colonized. Mite densities eventually become so high that plants die as a result of the feeding efforts of the population rather than of the individual.

One of the strategies for controlling tetranychids is the release of natural enemies, especially phytoseiid mites. Studies on feeding behaviour show that phytoseiids are not particularly voracious; only few encounters with prey result in prey consumption. However, it is not so much the predation rate as

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the increase in numbers that is responsible for the success of phytoseiids as biological control agents (Sabelis, 1985).

High population growth rates are thus decisive for the pest status of tetranychids as well as for their control by phytoseiids. This explains that so many publications have been devoted to life histories of both spider mites and predatory mites. Recently, these papers have been reviewed from the perspective of life-history evolution (Sabelis, 1991; Sabelis and Janssen, 1992). These reviews paved the way for a much simpler method for estimating intrinsic rates of increase, r_m .

Here, we first focus on r_m as one of the selection criteria for biological control agents. Subsequently, we summarize the review of phytoseiid life histories presented by Sabelis and Janssen (1992), and suggest a simple method for estimating r_m . Finally, we use a simple model of local dynamics of acarine predator-prey systems, to predict predator/prey ratios which are appropriate for biological control of tetranychids.

INTRINSIC RATES OF INCREASE AS SELECTION CRITERIA FOR PREDATORY MITES

Although many papers concern life table analyses of predatory mites and spider mites, it is still unclear what conclusions are to be drawn from their results in the framework of biological control. An argument against the use of life-history data, especially r_m , as a criterion for selection of suitable natural enemies, is that they are determined under conditions of unlimited prey supply and assume a stable age distribution. This would make their value under field conditions debatable. It has been suggested that selecting natural enemies based on their r_m is comparable to buying a car because of its high maximum speed, whereas it will only be used to drive slowly. In defence of using r_m as a selection criterion is that phytoseiids with an r_m equal to or higher than that of their tetranychid prey should at least have the potential of suppressing local prey populations. It remains to be shown to what extent a lower r_m can be compensated for by a higher predation rate.

What follows is a brief discussion of the population interactions that take place at a local spatial scale, because this shows why it is valuable — at least as a first step — to use r_m as one of the parameters for selection of biological control agents.

LOCAL DYNAMICS OF AN ACARINE PREDATOR-PREY SYSTEM

The following picture of local dynamics of an acarine predator-prey system is highly inspired by studies on the predator *Phytoseiulus persimilis* Athias-Henriot and its prey *Tetranychus urticae* Koch, but we will discuss the relevance for other systems later.

When a female spider mite finds a colony on a host plant, she will eat and produce offspring (and possibly web) on a very limited area. Upon reaching adulthood, her offspring will move to unoccupied sites on the same or an adjacent leaf. We will call the area occupied by spider mites and their waste products a prey patch. Such a patch gradually expands from its initial focus on one leaf until it covers an entire plant, or a group of neighbouring plants. It is within a prey patch that predator-prey dynamics appear to be strongly coupled, and our definition of the term local specifically concerns this spatial scale (Sabelis and Van der Meer, 1986).

As a result of the gradual expansion of a spider mite patch, the density of spider mites within the colony will stay fairly constant throughout the period of herbivore-plant interaction (Sabelis and Van der Meer, 1986). Thus, even though prey numbers increase exponentially in the course of host plant exploitation, prey density within a patch does not change dramatically, and provides constant feeding conditions for predators foraging in a patch. We will call this prey density the characteristic prey density (Sabelis, 1991). Characteristic prey densities may vary with spider mite species, but also with host plant species.

Phytoseiids restrict their searching activities to prey patches (Sabelis, 1981; Sabelis et al., 1984; Sabelis and Dicke, 1985). Within prey patches they will behave in a way similar to spider mites; they will gradually spread from their initial site of invasion. In doing so, predators will always meet characteristic prey densities. Over an extensive range of prey densities, the oviposition rate of phytoseiids is predominantly limited by the rate of food digestion of the predatory mite, and not by the amount of food available (Sabelis, 1990). The characteristic prey density falls within the range where the rate of oviposition is at its maximum (Sabelis and Van der Meer, 1986). The rate of oviposition of the phytoseiids is only limited by food supply at the very end of the period of predator-prey interaction, just before prey are eradicated. Essentially, the predators experience prey densities that allow for maximum oviposition rates during the major part of the interaction period, although the overall density of prey, viewed at a larger spatial scale, may be very low. Given some time to reach a stable age distribution, phytoseiid populations can grow at their potential rate during most of the interaction period, and thus intrinsic rates of increase are an adequate measure for population increase.

The predator-prey interaction within a prey patch typically lasts for several mite generations, and ends because the host plant dies as a result of overexploitation by spider mites, or because the spider mites are eradicated by phytoseiids (Sabelis, 1981; Sabelis and Van der Meer, 1986). Successful biological control aims at local eradication of the prey population, and we are therefore interested in the properties of phytoseiids that enable them to locally exterminate prey. For this purpose we use a simple model, based on characteristics presented in this section. Parameters for this model are ob-

tained from literature on phytoseiid life histories, as reviewed in the section below.

REVIEW OF THE LITERATURE

Criteria for data selection

The experimental set-up of life-history studies shows quite some variation. For example, various food types are used, studies are done at different temperatures, and life-history parameters are determined using either groups of females or isolated individuals. The way in which results are presented also shows considerable variation. Consequently, a clear set of criteria to select papers must be defined. To be included in this review, published data had to meet the following criteria: (1) an ample supply of tetranychids should be offered as prey; (2) temperature should fall within the range of 23 to 27°C, and should preferably equal 25°C; (3) sex ratio should be assessed in the offspring from isolated females; and (4) peak and/or mean rate of oviposition should be presented. The publications used for this review and a summary of the data are given in Sabelis and Janssen (1992).

Review of selected literature

Lewontin (1965) suggested that reproduction curves often have a triangular form. Indeed, the reproduction curve of spider mites generally has such a form (Sabelis, 1991). The rate of oviposition steeply rises to a peak soon after the onset of reproduction, and then decreases gradually. This triangular curve was also observed for phytoseiids, but only in less than 20% of the cases. The

Fig. 1. Daily oviposition rate ($n(x)$) of *Amblyseius idaeus* (dotted line, after Van Dinh et al., 1988), and a generalized reproduction schedule (drawn line). A , $T1$, $T2$, and W are age at first reproduction, at the beginning of peak oviposition, at the end of peak oviposition, and at the end of the reproductive period respectively. $n(T1)$ and $n(T2)$ are the peak oviposition rates at $T1$ and $T2$.

TABLE 1

Regression equations and correlation coefficients between life-history traits of phytoseiids and tetranychids

Independent variable	Dependent variable	<i>N</i>	<i>R</i> ²	Regression
Phytoseiids				
mean rate of oviposition	proportion daughters	42	0.432	$y = 0.60 + 0.056x$
mean rate of oviposition	fecundity	97	0.450	$y = 12.4 + 12.0x$
mean rate of oviposition	rate of development	87	0.619	$y = 0.074 + 0.028x$
mean rate of oviposition	intrinsic rate of increase	45	0.755	$y = 0.07 + 0.075x$
peak rate of oviposition	proportion daughters	28	0.213	$y = 0.61 + 0.04x$
peak rate of oviposition	fecundity	54	0.478	$y = 8.5 + 10.9x$
peak rate of oviposition	rate of development	52	0.576	$y = 0.083 + 0.019x$
peak rate of oviposition	intrinsic rate of increase	38	0.834	$y = 0.053 + 0.069x$
Tetranychids				
mean rate of oviposition	intrinsic rate of increase	24	0.680	$y = 0.122 + 0.018x$
peak rate of oviposition	intrinsic rate of increase	35	0.550	$y = 0.131 + 0.011x$

N stands for the number of data-pairs collected from the literature and *R*² is the square of the correlation coefficient.

more general form was a trapezoid, of which an example is shown in Fig. 1 (following Lewontin's notation as closely as possible). As in spider mites, the oviposition rate ($n(x)$) rapidly increases from the beginning of the reproductive period (A) until it reaches a peak at age $T1$, but then levels off, with a slight increase or decrease towards the end of this plateau phase ($T2$). It subsequently decreases until it becomes zero at the end of reproductive life (W). We define peak rate of oviposition as the rate of oviposition at age $T1$ (i.e., $n(T1)$), and the mean rate of oviposition ($\bar{n}(x)$) as the average over the entire reproduction period (from age A to W).

Relations between life-history parameters for spider mites are discussed in Sabelis (1991). Significant correlations between $n(T1)$ and rate of development, fecundity, or r_m were found. No correlation was found between $n(T1)$ and sex ratio, whereas the relation between $n(T1)$ and survival was not studied. The relations between $\bar{n}(x)$, $n(T1)$ and r_m are presented in Fig. 2 and Table 1. These relations appear to be linear.

For phytoseiid mites, significant linear correlations exist between $\bar{n}(x)$ or $n(T1)$ on the one hand, and the proportion of daughters, fecundity and rate of development on the other (Table 1). Hence, it may be expected that a correlation exists between $\bar{n}(x)$, $n(T1)$ and r_m . As shown in Table 1 and Fig. 2, this is indeed the case.

Because 50 to 70% of the prey material ingested by phytoseiids is converted into predator eggs, it is also expected that the predation rate (β) and the rate of oviposition are correlated. Data from the literature (Appendix 1) indeed show such a correlation (Fig. 3).

Fig. 2. Correlation between peak rate of oviposition and intrinsic rate of increase of mites. (a) Tetranychidae; regression equation: $y = 0.131 + 0.011x$ (35 data points, $R^2 = 0.550$). (b) Phytoseiidae; regression equation: $y = 0.053 + 0.069x$ (38 data points, $R^2 = 0.834$).

It can be concluded that life-history characteristics of phytoseiids covary in such a way that a linear relation exists between rates of oviposition (mean and peak) and the intrinsic rate of population increase. Why the r_m - n ($T1$) relation is linear, and how this and other relations between the life-history components evolved, is discussed elsewhere (Sabelis and Janssen, 1992).

A NEW METHOD FOR ESTIMATING r_m

That peak (or mean) rate of oviposition and r_m correlate so well is remarkable, the more so if we consider that the data analyzed here are collected by various authors at different places, and with some variation in experimental methods. The r_m is very sensitive to the interval between subsequent observations, especially early in the oviposition period (Sabelis, 1985; Van Dinh

Fig. 3. Correlation between predation rate and the mean rate of oviposition of female predatory mites. Regression equation: $y = 0.48 + 0.12x$ (36 data points, $R^2 = 0.569$).

et al., 1988). The data reviewed here are not standardized in this respect; in some of the papers, information on the interval between observations was even lacking. A fair amount of variation in the measurements of r_m is therefore expected. Hence, the actual relation between traits may even be stronger than found here.

Because such high percentages of the variance in r_m are explained by $\bar{n}(x)$ and $n(TI)$ (55% for spider mites and more than 75% for predatory mites, see Table 1), a simple method for estimating r_m is now possible. Clearly, it would save a considerable amount of time to measure the rate of oviposition and estimate r_m , rather than to establish a full life table. In addition, it is more convenient to measure $n(TI)$ rather than $\bar{n}(x)$, since it requires a shorter observation period.

Hence, we propose the following scenario. First, rear spider mites on the host plant species of interest and predatory mites on spider mites reared in this way. Second, isolate a sufficient number of females on an ample supply of the food source of interest to produce a synchronized egg wave of desired size. Food consists of fresh host plant material for spider mites, and host plant material with the characteristic prey density for phytoseiid mites. Third, observe the number of eggs produced per day from maturation until the rate of oviposition levels off. For spider mites, the observation period will amount to at least 4.5 days ($T - A = \text{ca. } 4.44$; Sabelis, 1991), but will usually be ca. 3 days longer to observe the levelling off. For predatory mites, the total observation period will last a few days longer than 1.7 days ($TI = 1.73 + 1.02A$, thus $TI - A = \text{ca. } 1.7$). Fourth, use the regression equations in Table 1 to estimate the intrinsic rates of increase.

We suggest to use these estimates as parameters in a simple population model of within-patch predator-prey dynamics. We show how this model can

be used to derive a simple rule for minimum, or threshold, predator/prey ratios required for successful biological control.

A SIMPLE MODEL FOR WITHIN-PATCH DYNAMICS

The essentials of within-patch dynamics can easily be captured in a simple mathematical model, proposed by Diekmann et al. (1988). Assuming that:

- (1) the predation rate is constant and within the plateau phase of the functional response curve,
  - (2) prey populations grow exponentially in the absence of predators,
  - (3) predator populations grow exponentially, and have no hyperpredators,
  - (4) populations have no age structure,
  - (5) predators do not disperse until prey are eradicated,
  - (6) prey and predator patches are founded by one individual, and subsequent immigration events have negligible effect on the dynamics,
  - (7) climatic conditions are constant,
- the within-patch dynamics can be represented by the following set of differential equations:

$$\begin{aligned}\frac{dx}{dt} &= \alpha x - \beta y \\ \frac{dy}{dt} &= \gamma y\end{aligned}\tag{1}$$

with x = number of prey, y = number of predators, α = rate of prey population growth, β = maximum rate of predation, and γ = rate of predator population growth.

The dynamical properties of this simple model are qualitatively similar to simulation models containing detailed biological information, such as age structure (Sabelis and Van der Meer, 1986). As discussed above and as shown in earlier papers (Sabelis, 1981; Sabelis and Laane, 1986; Sabelis and Van der Meer, 1986), most of the assumptions (numbers 1, 2, 3, 5, 6) are quite realistic. To what extent the absence of age structure and varying temperature will affect the quantitative predictions is a matter for further investigation.

This model can be used to determine whether a predator is at least capable of eliminating a local prey population. Elimination implies that the time from predator invasion to prey eradication (τ) should at least be finite ($\tau < \infty$). Integrating the differential equations of (1), and rewriting the resulting expressions yields a solution for τ (see Appendix 2 and Sabelis, 1992):

$$\tau = \frac{1}{\gamma - \alpha} \ln \left(1 + \frac{\gamma - \alpha}{\beta} x(0) \right)\tag{2}$$

with $x(0)$ being the number of spider mites at the time of predator invasion

(t_i). The interaction time τ is always finite when the growth rate of the predator is higher than that of the prey ($\gamma > \alpha$), but when $\gamma < \alpha$ the term between brackets in equation (2) should be between 0 and 1, and thus:

$$x(0) < \frac{\beta}{\gamma - \alpha} \quad (3)$$

The inverse of $x(0)$ represents the predator/prey ratio at the time of invasion (t_i). As a rule of thumb, this ratio $\{y(t_i)/x(t_i)\}$ should be larger than $(\gamma - \alpha)/\beta$ to achieve prey elimination within a finite timespan. Thus, when the (intrinsic) growth rates of prey and predator and the predation rate of the predator are known, it is possible to obtain an estimate of how many predators are needed to drive a local prey population to extinction. Since intrinsic rates of increase can easily be obtained (see above), the only unknown parameter is the predation rate, but, as we have shown above, this parameter is correlated with $\bar{n}(x)$. Substitution of the regression equation of β versus $\bar{n}(x)$ ($\beta = 3.42 + 4.85 \bar{n}(x)$) in the regression of $\bar{n}(x)$ versus r_m ($\bar{n}(x) = -0.16 + 9.75 \gamma$) gives an expression for β as a function of γ . This can subsequently be used to cancel out β from equation (3).

A further adjustment should be made because the data concern adult female predators feeding on prey eggs only. Under a stable age distribution, adult female predators constitute about 17.2% of a population, whereas all other feeding stages represent 34.6% (Carey and Krainacker, 1988). The consumption of prey eggs by the other feeding predator stages is 0.45 of that of the adult females (Laing, 1968; Ma and Laing, 1973; Tanigoshi and McMurtry, 1977; Shih et al., 1979; Sabelis, 1981; Lababidi, 1988; Van Dinh et al., 1988). Assuming that predation on adult female spider mites is negligible, and that predation on all other stages is equal to that on eggs, the value of β can be obtained from:

$$\beta = 0.172\beta_f + 0.346\beta_j = 0.33\beta_f \quad (4)$$

with β_f = average predation rate of adult females, and β_j = average predation rate of juveniles and adult males. Thus, the predation rate in the population model should be about 1/3 of the value that emerges from the regression equations. Substituting the expression of β as function of γ into equation (3), after multiplying with 1/3, the 'threshold-ratio' rule can now be expressed in terms of the intrinsic rates of increase of predator and prey:

$$\frac{y(t_i)}{x(t_i)} > \frac{\alpha - \gamma}{0.87 + 15.8\gamma} \quad (5)$$

A graphical representation of this condition is given in Fig. 4. It shows the predator/prey ratio as a function of α for various values of γ using equation (5). The lines in the graph indicate when the predator/prey ratio is exactly

Fig. 4. The threshold predator/prey ratio as a function of α for various values of γ . The parameters α and γ are the r_m s of the tetranychid and phytoseiid respectively. When the predator/prey ratio exceeds that of the drawn line, prey in the patch will eventually be eradicated. See text for further explanation.

equal to the right-hand side of this equation. For a predator to exterminate a local prey population, the ratio should thus lie above this threshold. It can be seen that threshold values increase with increasing α . This is not surprising, since — other things being equal — higher growth rates of the prey will demand a release of a larger number of predators in order to achieve control. Figure 4 also shows, as expected, that increasing values of the predator's r_m (γ) lead to lower threshold predator/prey ratios.

What lesson can we draw from Fig. 4 for the selection of phytoseiids for biological control of tetranychid mites? In biological control systems where predators are used as a biological pesticide to exterminate a local prey population (i.e., the current practice in greenhouses and seasonal cropping systems such as strawberry), experience shows that adequate predator/prey ratios at release are usually between 0.017 and 0.05. For these ratios, the growth rate of phytoseiids needs not be as high as that of the tetranychid pest (Fig. 4). For example, with a predator/prey ratio of 0.05, and an intrinsic rate of increase of the prey of 0.4, the minimum r_m of a successful natural enemy is only slightly higher than 0.2, thus only half of that of the prey. Hence, a low r_m of the predator can be compensated by releasing larger quantities of phytoseiids in such a way that the predator/prey ratio at the time of release exceeds the threshold ratio given in Fig. 4.

When control is aimed at larger spatial and temporal scales, our model is inadequate for predicting predator/prey ratios at release. This is because dispersal between local populations becomes decisive to the outcome of the interaction, and this process is not included in the model. However, our model can be used to evaluate the success on a local scale, assuming that immigration and emigration are negligible at the spatial and temporal scale considered (Sabelis and Van der Meer, 1986). To this end, estimates of predator/prey ratios in local field populations serve to initialize the model, which can

Fig. 5. The minimum predator/prey ratio necessary to keep the increase in damage during the interaction period limited to I , for various values of r_m of prey and predator (α and γ). See text for further explanation.

then be used to calculate to what extent the prey population will increase before they are wiped out by the predator. For growers, such a calculation is not applicable, because they are primarily interested in the amount of damage inflicted upon the crop. However, in the model, mite numbers can be converted into a measure of damage by calculating the number of spider-mite-days over the total interaction period. This damage index can be derived by integrating the prey equation over the period to prey extinction τ (see Appendix 2). Figure 5 shows that the relative increase in damage (I) increases with α , and decreases with γ and the predator/prey ratio. For example, with a rate of increase of 0.4 for the prey (α) and 0.2 for the predator (γ), a predator/prey ratio of ca. 0.08, or 1 predator per 12.5 prey, would yield a two-fold increase in damage before the prey are exterminated. If a ten-fold increase in damage can be accepted, the predator/prey ratio should be about 0.06, or 1 predator per 16.7 prey. If the expected increase in damage is too high, farmers can take measures by locally adding extra predators or by locally applying pesticides. This example also shows that the increase in damage critically depends on the predator/prey ratio. A decrease in this ratio to 75% would result in a five-fold increase in damage!

CONCLUSIONS AND DISCUSSION

How to estimate r_m in a simple way

Our literature review shows that many life-history parameters, and predation rates, are closely related to the rate of oviposition. This paves the way to

developing quick experiments that yield estimates of r_m , or other life-history parameters. This method is subject to statistical error, as the correlations are not perfect, and the regressions are based on a subsample of the family of Phytoseiidae. However, whether detailed observations on all life-history traits result in a more accurate estimate of r_m remains to be seen. We feel that, to date, insufficient account is given to the problems involved in obtaining correct estimates. For one thing, the cultures of phytoseiids often originate from small samples of a restricted area, and are subjected to selection imposed by culture conditions. Whether these cultures harbour sufficient genetic variation to be representative for a field population remains questionable. Moreover, only life-history data collected with extreme care (necessitating frequent observations over extensive periods) will yield an accurate estimate of r_m (see Van Dinh et al., 1988). It remains to be shown that the correlative method is inferior to in-depth life-history studies in a meaningful way, i.e., expressed in terms of the effect on threshold predator/prey ratios. We do not advocate the correlative method as being the best, but, for the time being, it is the most simple method.

How to use r_m in evaluating natural enemies

Selection of predators for biological control usually starts with collecting natural enemies from areas with climatic conditions matching to the conditions prevailing in the target prey habitat. Subsequently, a hierarchical sequence of questions has to be answered:

1. Does the predator feed on the target prey?
2. Does the predator reproduce on this diet?
3. Is its intrinsic rate of increase and predation rate sufficient to suppress local prey populations?
4. Are there perspectives for developing mass-rearing techniques?

We suggest to answer the first two questions by an experiment with young female predators, according to the scenario discussed earlier. The results of this experiment can be used to answer the third question, using the regressions and the 'threshold-ratio' rule derived from the model presented in this paper. To answer the fourth question, one should realize that a trade-off exists between r_m and the threshold predator/prey ratio required for local control of the prey population; the higher r_m , the lower the threshold-ratio, the smaller the size of the mass culture can be.

How to use r_m in determining adequate predator/prey ratios

A general feature of inoculative biological control is that the prey population, and hence, also the damage, will increase for some time after introduction of the predator. The extent to which damage will increase depends on the current predator/prey ratio. Our model can be used to calculate the increase

in damage (I) as a function of the predator/prey ratio, and the r_m of predator and prey (Fig. 5). When the existing predator/prey ratio would lead to an unacceptable increase in damage, the grower could act by taking additional control measures. Thus the model serves as a tool for estimating adequate predator/prey ratios when the aim is to eradicate prey and to use predators as a 'biological pesticide'.

However, it should be realized that the model only applies to the dynamics within a local population, under conditions where migration rates between populations are negligible (i.e., low relative to the r_m of prey and predator). When the aim is to establish a persistent predator population on a larger spatial scale, it becomes increasingly important to consider passive dispersal of prey and predator, the ability to find new prey patches, prey selectivity (Janssen et al., 1990), and the use of alternative food (McMurtry, 1982, 1992; Murdoch et al., 1985).

Local persistence is unlikely in the case of a strongly coupled one-predator/one-prey system (Nachman, 1981; Takafuji et al., 1983; Sabelis et al., 1991; see Nachman, 1987a,b and Sabelis et al., 1991 for mechanisms leading to regional, or metapopulation persistence), but it may arise when local predator populations can rely on alternative food (such as pollen, nectar, or other, arthropod, prey) when the target prey is absent. Predators are thus more likely to be present on the plant in sufficient numbers to suppress newly-formed prey colonies (McMurtry, 1982, 1992; Tanigoshi, 1982). In fact, this can be viewed as a special case of a one-predator/one-prey interaction, where the initial predator/prey ratio is extremely high, the more so when predators preferably feed on the target prey. It can be seen from Figs. 4 and 5 that predators with low r_m may then suffice to obtain local prey extinction. An example may be the successful control of thrips in sweet pepper by *Amblyseius cucumeris* (Oudemans), a predator with a low r_m , and ability to persist on sweet pepper pollen (Van Rijn and Sabelis, 1990; Van Rijn and Van Houten, 1991).

How to evaluate the usefulness of the predator-prey model

The method described in this paper is by no means meant as a dogma. We advocate testing the model in two essentially different ways. First, in-depth theoretical research should test the robustness of the model and the 'threshold-ratio' rule, for example by modelling age structure, food selectivity, immigration and emigration, and its effect on local population dynamics and predator/prey ratios required for local control. Second, the 'threshold-ratio' rule as such can be tested in the practice of biological control. Farmers can easily obtain information on predator/prey ratios and assess if and when local prey extinction occurs. The theoretical and practical tests of the 'threshold-ratio' rule each have their own merit, as they are independent and test

different questions, but both are needed to provide a scientific basis for assessing the adequacy of predator/prey ratios.

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APPENDIX 1

Mean oviposition rates and predation rates of phytoseiids

Species	Mean	Pred.	Reference
<i>A. anonymus</i>	2.27	12.4	Van Dinh et al. (1988)
<i>A. bibens</i>	2.15	13.4	Blommers (1976)
<i>A. bibens</i>	3.10	16.8	Lababidi (1988)
<i>A. californicus</i>	2.61	10.1	Friese and Gilstrap (1982)
<i>A. chilensis</i>	3.10	16.2	Ma and Laing (1973)
<i>A. cucumeris</i>	1.80	11.9	Lababidi (1988)
<i>A. fallacis</i>	2.20	15.7	Lababidi (1988)
<i>A. fallacis</i>	3.20	10.6	Smith and Newson (1970 a&b)
<i>A. idaeus</i>	2.35	12.8	Van Dinh et al. (1988)
<i>A. longispinosus</i>	2.30	17.6	Lababidi (1988)
<i>A. longispinosus</i>	1.39	10.7	Shih and Shieh (1979)
<i>A. mckenzie</i>	2.00	9.8	Lababidi (1988)
<i>A. ovalis</i>	2.42	17.2	C.I.T. Shih and P.H. Shu (unpubl. data, 1984)
<i>P. macropilis</i>	2.62	6.1	Prasad (1967)
<i>P. macropilis</i>	1.90	9.5	Shih et al. (1979)
<i>P. persimilis</i>	0.20	9.0	Ashihara et al. (1978)
<i>P. persimilis</i>	0.20	8.5	Ashihara et al. (1978)
<i>P. persimilis</i>	1.90	28.1	Ashihara et al. (1978)
<i>P. persimilis</i>	3.20	22.1	Ashihara et al. (1978)
<i>P. persimilis</i>	3.50	24.6	Ashihara et al. (1978)
<i>P. persimilis</i>	4.50	28.1	Ashihara et al. (1978)
<i>P. persimilis</i>	0.00	0.0	Ashihara et al. (1978)
<i>P. persimilis</i>	3.80	25.0	Friese and Gilstrap (1982)
<i>P. persimilis</i>	3.50	24.6	Lababidi (1988)
<i>Ph. hawaiiensis</i>	0.87	11.9	Sanderson and McMurtry (1984)
<i>T. annectens</i>	1.06	9.5	Badii et al. (1990)
<i>T. bambusae</i>	1.70	8.4	Saito (1990)
<i>T. floridanus</i>	1.97	12.2	Tanigoshi and McMurtry (1977)
<i>T. occidentalis</i>	1.00	8.4	Badii et al. (1990)
<i>T. occidentalis</i>	2.40	12.0	Bruce-Oliver and Hoy (1990)
<i>T. occidentalis</i>	1.23	14.4	Friese and Gilstrap (1982)
<i>T. occidentalis</i>	1.90	15.8	Lababidi (1988)
<i>T. pini</i>	0.95	1.9	Charlet and McMurtry (1977)

<i>T. porresi</i>	0.59	7.9	Badii et al. (1990)
<i>T. validus</i>	1.10	2.8	Charlet and McMurtry (1977)

Mean indicates mean rate of oviposition, and Pred. stands for predation rate on prey eggs.

APPENDIX 2

The system of two first-order equations

$$\begin{aligned}\frac{dx}{dt} &= \alpha x - \beta y \\ \frac{dy}{dt} &= \gamma y\end{aligned}\tag{A1}$$

can be reduced by the elimination method to a single second-order equation in $x(t)$, which has the general solution for $x(t)$ (Edelstein-Keshet, 1988, p. 133):

$$x(t) = c_1 e^{\alpha t} + c_2 e^{\gamma t}\tag{A2}$$

It follows directly that for $t=0$, $x(0) = c_1 + c_2$. To determine c_2 , first rewrite the prey equation of (A1) into the following form:

$$y(t) = -\frac{1}{\beta} \left(\frac{dx(t)}{dt} - \alpha x(t) \right)\tag{A3}$$

Substitution of the general solution of $x(t)$ (A2) into the above equation yields:

$$y(t) = -\frac{\gamma - \alpha}{\beta} e^{\gamma t} c_2\tag{A4}$$

Because $y(0) = 1$, it follows that $c_2 = -\beta / (\gamma - \alpha)$. Thus, the two first-order equations (A1) have the following solution:

$$\begin{aligned}x(t) &= x(0) e^{\alpha t} - \frac{\beta}{\gamma - \alpha} (e^{\gamma t} - e^{\alpha t}) \\ y(t) &= y(0) e^{\gamma t}\end{aligned}\tag{A5}$$

with $y(0) = 1$, $x(0) = e^{\alpha t_i}$, t_i = time of predator invasion and t = time since predator invasion.

All prey are eradicated at the end of the interaction period (τ), hence $x(\tau) = 0$. Equation A5 can then be rewritten to find a solution for τ :

$$\tau = \frac{1}{\gamma - \alpha} \ln \left(1 + \frac{\gamma - \alpha}{\beta} x(0) \right)\tag{A6}$$

This expression has been used in this paper to determine under which conditions the interaction period is finite ($\tau < \infty$).

To determine the increase in damage in the period from release of the predator until prey extinction, the cumulative number of mite-days during the interaction period can be used, i.e., the area under the prey population growth curve. The latter is obtained by integrating the first expression of A7 over the total interaction period:

$$\int_0^{\tau} x(t) dt = \int_0^{\tau} x(0) e^{\alpha t} dt - \int_0^{\tau} \frac{\beta}{\gamma - \alpha} e^{\gamma t} dt + \int_0^{\tau} \frac{\beta}{\gamma - \alpha} e^{\alpha t} dt\tag{A7}$$

This results in an expression for the cumulative number of mite-days:

$$\frac{1}{\alpha} \left\{ x(0) + \frac{\beta}{\gamma - \alpha} (e^{\alpha\tau} - 1) \right\} - \frac{\beta}{\gamma(\gamma - \alpha)} (e^{\gamma\tau} - 1) \quad (\text{A8})$$

The amount of damage at the start of the interaction period (t_i) can be obtained by:

$$\int_0^{t_i} e^{\alpha t} dt = \frac{1}{\alpha} (x(0) - 1) \quad (\text{A9})$$

Hence, the relative increase in damage (I) during the interaction period is obtained by dividing expression A8 by A9:

$$I = \frac{1}{x(0) - 1} \left\{ \left(x(0) + \frac{\beta}{\gamma - \alpha} (e^{\alpha\tau} - 1) \right) - \frac{\alpha\beta}{\gamma(\gamma - \alpha)} (e^{\gamma\tau} - 1) \right\} \quad (\text{A10})$$

The parameter β can be eliminated from these equations by using the regression equations given in this paper. Subsequently, with values for α , γ , and the allowable increase in damage (I), equations A6 and A10 can be iterated to yield the minimum predator/prey ratio to keep the increase in damage limited. The results of this iteration are presented in Fig. 5.

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