Experimental & Applied Acarology, 14 (1992) 261-291
Elsevier Science Publishers B.V., Amsterdam

Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence

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ABSTRACT

Walde, S.J., Nyrop, J.P. and Hardman, J.M., 1992. Dynamics of *Panonychus ulmi* and *Typhlodromus pyri*: factors contributing to persistence. *Exp. Appl. Acarol.*, 14: 261-291.

We addressed the question of persistence of predator and prey in a biological control system by examining temporal patterns of *Panonychus ulmi* (Koch) and its predator, *Typhlodromus pyri* Scheuten at two geographic locations and at two spatial scales. At the scale of an orchard, both *P. ulmi* and *T. pyri* were persistent over the time frame of 6 years. At the scale of an individual tree, *T. pyri* appeared to be more persistent than its prey, *P. ulmi*. We used a simulation model of single populations of *P. ulmi* and *T. pyri* to determine which of several aspects of the biology of the two species could contribute to such a pattern. Spatial incongruity between predator and prey was essential for persistence of both species. The generalist food habit of *T. pyri* probably contributes to the persistence of *T. pyri* on individual trees, and may cause occasional extinction of *P. ulmi* at this spatial scale. The presence of alternate food is likely an essential element for successful biological control in this system. Cannibalism by *T. pyri* results in higher prey densities, that is, it is detrimental to the biological control of *P. ulmi*, but has no effect on the relative persistence of the two species.

INTRODUCTION

Most mathematical theories pertaining to biological control systems have two central objectives: (1) to explain the stability of the natural enemy–pest interaction, and (2) to explain how the natural enemy produces a low pest equilibrium density (Murdoch, 1989). The issue of stability in biological control systems has been the subject of controversy, the debate centering on whether stability is a necessary component of successful biological control systems, and if so, what factors are responsible for this stability (Hassell, 1985; Murdoch et al., 1985).

A large body of theory directed at explaining predator–prey or parasitoid–

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host interactions in general, and biological control systems in particular has been based on the Nicholson–Bailey parasitoid–host models, (e.g. Hassell, 1978). A variety of factors were found to contribute to stability in these models, including intraspecific competition among hosts or among parasitoids, sigmoid functional responses, refuges and parasitoid aggregative behaviour. Of these, aggregation, coupled with resource limitation for the prey were proposed as the most likely sources of stability in biological control systems (Beddington et al., 1978). A parallel set of ideas, although with the mathematics more recently developed (e.g. Diekmann et al., 1988; Reeve, 1988; Sabelis and Diekmann, 1988), suggests that local populations may be subject to periodic extinctions, and that dispersal among these populations may be the key to global stability.

Thus much of the debate has centered on whether local extinctions occur (den Boer, 1968), on whether parasitoid or predator aggregative behaviour occurs (Reeve and Murdoch, 1985; Stiling, 1987; Walde and Murdoch, 1988) and on whether this behaviour is likely to produce stable interactions in successful biological control (Murdoch and Stewart-Oaten, 1989). Much of the work on local extinctions, dispersal and the dynamics of meta-populations has been stimulated by or based on experimental work on phytophagous mites and their phytoseid predators. The proposed scenario, based mostly on *Tetranychus urticae* and *Phytoseiulus persimilis* Athias-Henriot, is as follows (e.g. Diekmann et al.,1988; Nachman, 1988): The prey colonizes a plant and begins to reproduce. If left alone, the colony will decimate its food supply and crash, with some individuals dispersing to start new colonies. If invaded by the predator, the predator will decimate the colony, remaining until all individuals are eaten or have dispersed, thus again causing a local extinction. The system remains stable only on a larger spatial scale, and its persistence depends on the relative dispersal rates of the prey and predator, as well as other characteristics such as the form of the predator functional and numerical responses.

This paper was stimulated by studies of a phytophagous–phytoseid mite system, *Panonychus ulmi* (Koch) and *Typhlodromus pyri* Scheuten in apple orchards in eastern Canada and the northeastern USA, that did not appear to conform to either the classical pattern of stability or the pattern of extinctions generated by metapopulation dynamics. We support our contention that we may have a different type of dynamics in this predator–prey system with field data from New York, USA and Nova Scotia, Canada. We then explore various possible explanations for the dynamic patterns with a simulation model of the *P. ulmi–T. pyri* interaction.

THE *PANONYCHUS ULMI–TYPHLODROMUS PYRI* INTERACTION

In eastern North American commercial apple orchards under insect control regimes that do not interfere with the predator, *T. pyri* can maintain *P. ulmi* at densities that are acceptable from an economic standpoint, that is, it can be considered a case of successful biological control. *Panonychus ulmi* is thus largely a pesticide-induced pest, but one that can cause serious economic harm in commercial orchards. *Panonychus ulmi* overwinters on the bark of apple trees, and passes through 3 to 5 (Nova Scotia) or 5 to 7 (New York) generations per year. *Typhlodromus pyri* is frequently the dominant phytoseid in these orchards. *Panonychus ulmi* is a preferred and important prey, with various developmental stages showing differential susceptibilities to predation. The development time of *T. pyri* is roughly the same as that of *P. ulmi*, but its fecundity considerably lower. Thus its numerical response is not particularly dramatic, and for this and other reasons, its ability to control *P. ulmi*, has been doubted.

Other species also interact with the *T. pyri–P. ulmi* system, their importance varying, depending on location and pest control practices. Other predators of *P. ulmi* are frequently present, the most important usually being the stigmaeid, *Zetzellia mali*. *Typhlodromus pyri* does not feed exclusively on *P. ulmi*, other significant food sources in New York and Nova Scotia orchards include pollen and the apple rust mite, *Aculus schlechtendali*, both most important early in the season.

TEMPORAL PATTERNS IN THE FIELD

Here we present data on the temporal dynamics of *P. ulmi* and *T. pyri* in apple orchards in Nova Scotia, Canada and New York, USA. First we provide data that strongly suggest that *T. pyri* can and does control *P. ulmi* populations in orchards in this region. Then we show that in such orchards *T. pyri* appears not to go extinct, either at the spatial scale of an orchard or that of individual trees. In contrast, while *P. ulmi* also persists at the spatial scale of an orchard, our data suggest that it may sometimes go locally extinct on trees.

Biological control by T. pyri

While workers in New Zealand, Europe and Australia (Collyer, 1980; Cranham and Solomon, 1981; Readshaw et al., 1982) had suggested that *P. ulmi* might be controlled by *T. pyri*, the effectiveness of this predator was doubted by some researchers in North America for many years. *Typhlodromus pyri* was thought to have an inadequate numerical response to *P. ulmi*, and to have a spatial distribution within leaves that was also not sufficiently overlapping (Chant, 1959).

An experiment was begun in 1985 in New York state to explicitly test the idea that effective biological control of *P. ulmi* could be obtained in eastern North America with *T. pyri*. The experiment was conducted in two orchards (Crittendon and Darrow), which contained seven different disease-resistant varieties of apple, all on semi-dwarf rootstock, and planted in 1978. All sampling was done on the cultivar 'Liberty'. *Typhlodromus pyri* was introduced to the Crittendon orchard in 1985 and the Darrow orchard in 1986 by attaching *T. pyri*-containing foliage or burlap bands to the trees. In 1986 and 1987, each orchard was divided into four blocks, of which half received insecticide treatments designed to have little or no impact on *T. pyri*, and half received treatments that virtually eliminated these predators. Five trees were sampled in each block, with samples of 20 to 25 leaves per tree taken at approximately weekly intervals and examined microscopically for *P. ulmi* and *T. pyri*.

Comparison of *P. ulmi* population densities in the absence and presence of the predator show that trees without *T. pyri* had maximum densities from 6 to 12 times higher in the first year and 18 to 30 times higher the second year (Fig. 1). Although insecticide treatments are not perfect tests for predator efficacy, it was quite obvious that removal of *T. pyri* had a dramatic effect on *P. ulmi* populations: *P. ulmi* was kept below economically acceptable levels when *T. pyri* was present and not when it was removed by insecticides. No other phytoseid predators were present in these orchards. *Zetzellia mali* (Stigmaeidae) was present, but unlikely to have caused differences, since their presence was inconsistently associated with the suppression of *P. ulmi*. Maximum densities of *Z. mali* were higher in the pesticide-treated blocks (Crittendon: 0.34/leaf, Darrow: 2.5/leaf) than in the control blocks (Crittendon: 0.08/leaf, Darrow: 0.24/leaf).

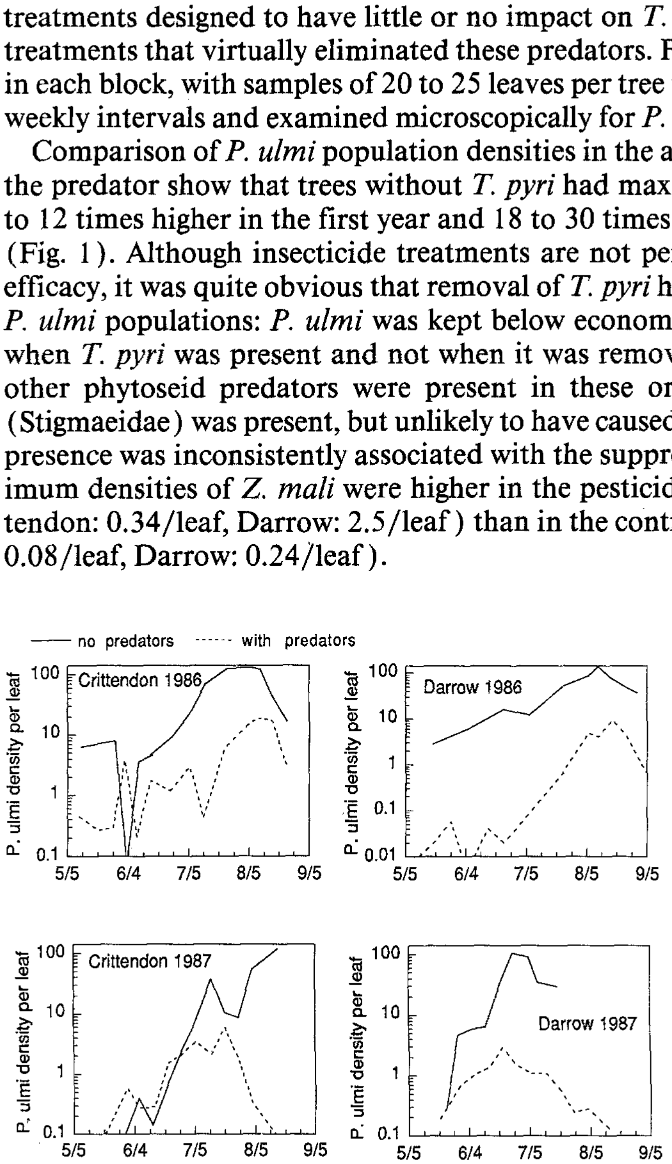


Fig. 1. Effect of *Typhlodromus pyri* on the growth of *Panonychus ulmi* populations at two New York sites during two consecutive years. The predator *T. pyri* was excluded via insecticide applications.

Persistence

The hypothesis that the dynamics of phytophagous mites and their predators are characterized by local extinctions is supported by considerable experimental evidence as cited above, but almost all of this evidence comes from laboratory or glasshouse experiments. It is possible that different dynamics characterize populations under field conditions, and thus we examined the evidence for persistence versus extinction in field populations at two different spatial scales, at the level of an orchard block and at the level of an individual tree, and in two regions of eastern North America.

It is extremely difficult to establish that extinction has occurred when one cannot examine every leaf on a tree, let alone in an orchard. Thus we used an operational definition of extinction; we called a population extinct if no individuals were counted in any sample throughout an entire season. This method certainly has shortcomings. On the one hand, there may have been mites on the trees that we missed in our samples, i.e. our extinctions might not be true extinctions. To ascertain at a probability of 0.05, that not one leaf on a mature tree contained a single mite would require the inspection of some 30 000 leaves on that tree (Kuno, 1991). Clearly this kind of a sampling regime is rarely possible, and thus we cannot be sure that there were no mites on the trees. On the other hand, we could at the same time be missing extinctions, as populations could be disappearing and recolonizing within a season. Thus our 'extinctions' should be interpreted with caution; what they certainly represent is reduction to very low densities.

New York orchards

Both Crittendon and Darrow orchards were sampled for an additional 4 years, with only three treatments of an organophosphate (azinphosmethyl) per year. *Typhlodromus pyri* in New York state are highly resistant to organophosphates, and so disruption of the *T. pyri–P. ulmi* interaction should have been minimal. The sampling schedule was the same as above.

The pattern of density and persistence at the spatial scale of the orchard is shown in Fig. 2 as the average of the sample trees. In the Darrow orchard, both *P. ulmi* and *T. pyri* were persistent over the entire 5-year period. In the Crittendon orchard, no *P. ulmi* were found in any of the samples of the five target trees in 1989. However, samples from other trees in the orchard contained *P. ulmi* on these same sample dates, and thus although the density of *P. ulmi* at Crittendon in 1989 was obviously very low, the population at this spatial scale was not extinct. *Typhlodromus pyri* was persistent in this orchard as well.

When the population trends are examined for each tree in the two orchards, the pattern remains the same for *T. pyri*. The predator is present every year on every tree and there is little evidence that it is tending to zero. The pattern

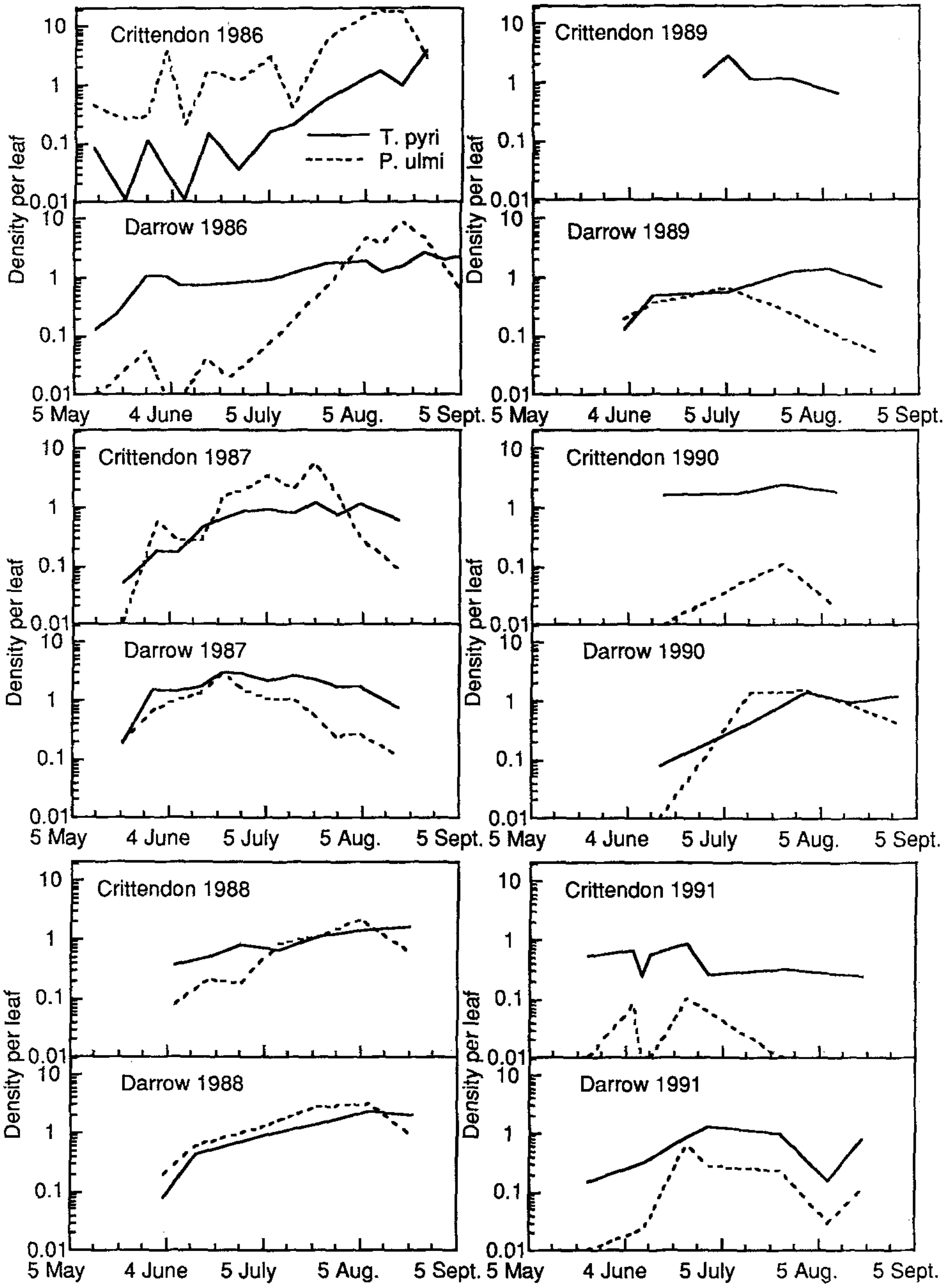


Fig. 2. Temporal change in density of *Typhlodromus pyri* and *Panonychus ulmi* populations at two New York sites during a six-year period. Population abundances were estimated using the same five trees each year. Estimates of *P. ulmi* density were zero for in all five trees throughout the season in 1989 at Crittendon, and were zero for two of five trees at Crittendon through 1990.

for *P. ulmi* is somewhat different. At Darrow *P. ulmi* was found on all trees in all years. However, at Crittendon five of five trees had counts of zero *P. ulmi* in 1989 and two of five trees had apparently no *P. ulmi* in 1990.

Nova Scotia experimental orchard

A field experiment aimed at testing whether or not the number of interacting populations influences the dynamics of phytophagous mite populations in the field was conducted in the Annapolis Valley of Nova Scotia, Canada. Two aspects of the dynamics of the pest and predator populations were emphasized, density and probability of extinction.

Whips of a scab-resistant strain of MacIntosh, Nova Mac, were planted in the spring of 1989 in groups of size 1, 4 (2×2) or 16 (4×4) trees, and inoculated with *P. ulmi* by attaching infested leaves to the trees. Within groups, trees were 1.5 to 2 m apart, and groups were a minimum of 20 m apart. The densities of the populations of *P. ulmi* and *T. pyri* were estimated by examining leaves in the laboratory. No insecticides or fungicides were applied to the trees.

In the first season, it was found that *P. ulmi* densities were highest in the largest groups, and that there was a tendency (although not statistically significant, $P=0.12$) for populations to persist longer on trees in the larger groups than on isolated trees (Walde, 1991). Half of the original trees were followed for a second season without further manipulation, and these results are reported here.

Thus in the second year, the experimental design consisted of ten single trees (G-1), four groups of four trees (G-4), and four groups of 16 trees (G-16). Again, no insecticides or fungicides were applied to the orchard. Samples of seven leaves were taken from each tree on seven dates at approximately 2-week intervals throughout the growing season, and examined for *P. ulmi* and *T. pyri*.

Trees in groups of 16 again had higher densities of *P. ulmi* than trees in smaller groups (Fig. 3). Cumulative mite-days per leaf (2.99, 0.96 and 8.85 for G-1, G-4 and G-16 trees, respectively) were significantly higher for G-16 trees ($P<0.001$). There was no significant difference among group sizes in number of *T. pyri* (Fig. 3). Thus the pattern produced by varying the number of interacting populations persisted through a second season.

As in virtually all orchards without pesticide treatments, *P. ulmi* densities were very low. In the second season, no *P. ulmi* were found on any date on nearly half of the experimental trees. Although it is impossible to say that there were actually no *P. ulmi* on these trees without having examined every leaf, it is obvious that these populations were very close to if not actually at zero. Thus we tentatively classify these populations as having gone extinct the first year, and not having been recolonized the second year. The proportion of trees in this category were not distributed equally among the group sizes:

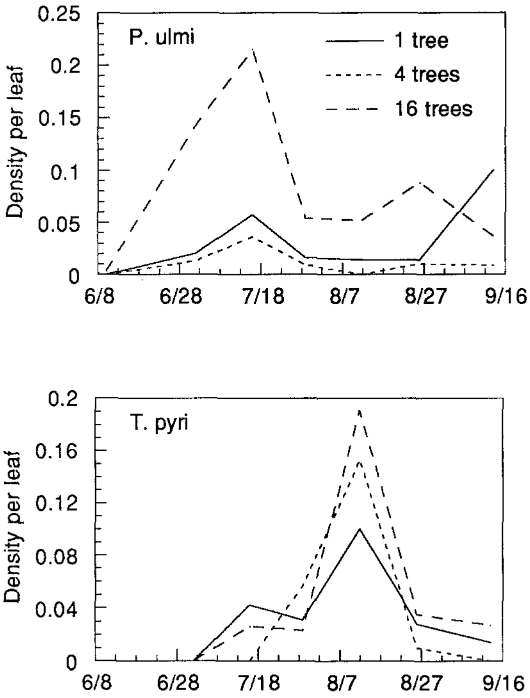


Fig. 3. Effect of manipulating patch size (number of trees in the group) on population abundance of *Panonychus ulmi* and *Typhlodromus pyri* in Nova Scotia for the season of 1990.

70% of the G-1 trees and 75% of the G-4 trees had no *P. ulmi* in any sample, while only 33% of the G-16 trees fell into this category. This difference was statistically significant (likelihood ratio chi-square test, $P=0.003$).

Thus we have confirmation of the pattern that was seen in the first season of this experiment: higher mean densities and apparently greater persistence of *P. ulmi* in trees that had more interaction with other populations.

This contrasts with the pattern seen for the predator. *Typhlodromus pyri* showed significantly higher levels of persistence at the spatial scale of a tree than did *P. ulmi*. Only 16% of the trees had no *T. pyri* through the season as compared with 45% with no *P. ulmi* (likelihood ratio chi-square test, $P<0.001$). There were no significant differences among group sizes in persistence of *T. pyri*, with 30%, 13% and 15% of the G-1, G-4 and G-16 populations showing counts of zero throughout the season (likelihood ratio chi-square test, $P=0.49$).

These results, then, confirm the patterns seen in New York, where both *P. ulmi* and *T. pyri* seem to be persistent at the spatial scale of an orchard and *T. pyri* is more persistent at the scale of a tree than its primary prey, *P. ulmi*. At this spatial scale, these patterns contrast with the classical view of successful biological control, where both predator and prey coexist at low equilibria. But the pattern, in particular the greater persistence of *T. pyri*, also does not fit the repeated colonization and extinction scenario suggested by observations on *P. persimilis* and *T. urticae*. In the following section we explore several aspects of the biology of the *T. pyri*–*P. ulmi* interaction that may contribute to the observed pattern of dynamics.

MECHANISMS UNDERLYING TEMPORAL DYNAMICS

While it is possible that a metapopulation structure consisting of populations defined at the spatial scale of individual trees could lead to the observed dynamics at the scale of an orchard, the pattern observed on individual trees is not as easily explained. Most metapopulation models to date do not allow for persistence of the predator within a patch in the absence of the prey (see Vandermeer (1973) for an exception). We were thus interested in asking whether persistence might arise or be influenced by other processes inherent to the *T. pyri*–*P. ulmi* system. In particular we wished to know whether (1) the foraging behaviour and feeding habits of *T. pyri*, (2) cannibalism by *T. pyri*, and (3) differences in the overwintering survival of *T. pyri* and *P. ulmi*, in conjunction with other system processes could lead to a persistent predator–prey system. To answer these questions we constructed a simulation model of *T. pyri*–*P. ulmi* dynamics in apple trees and performed experiments with the model. In the remainder of the paper we will describe the model and its validation and present results from experiments conducted with the model.

Model description

Overview of model

The model was comprised of single *T. pyri* and *P. ulmi* populations each with six developmental stages: eggs, larvae, protonymphs, deutonymphs, preovipositional adults, and ovipositing adults. Thus there was no structure that allows for extinction and subsequent colonization of prey or predator. The spatial distributions of predator and prey were modelled as random with respect to one another. Phenological development was temperature driven. Predation was stage specific: mixed age classes of prey were consumed by mixed age classes of predators. Egg production by *T. pyri* depended on prey consumption and temperature. Egg production by *P. ulmi* was dependent on temperature, time of season, density of motile *P. ulmi* and cumulative mite-days. Sex ratios for both prey and predators were assumed to be a constant 7:3 (female:male). Survival rates of the *P. ulmi* motile stages and the rate of *P. ulmi* reproduction were density dependent; both began to decline at a threshold of 35 motiles per leaf.

Cannibalism by predators was included by considering predator larvae and protonymphs as prey items. Alternate food was provided to predators by assuming certain minimal ovipositional requirements were met when insufficient *P. ulmi* were consumed. Overwintering mortality was incorporated by reducing initial prey and predator densities in the succeeding year. Absent from the model were predator starvation and food consumption effects on predator development.

Phenological development

The model simulated daily changes in the density and age structure of the *T. pyri* and *P. ulmi* populations from 1 March to 31 October. The predator population included 20 age classes each of eggs, immatures and adults. Within the *T. pyri* immatures, classes 1–3 were larvae, classes 4–12 were protonymphs and classes 13–20 were deutonymphs. The prey population included 30 age classes of winter eggs and 20 classes each of summer eggs, immatures and adults. Development was driven by hourly mean temperature which was a sinusoidal function of daily mean temperature and temperature amplitude. Developmental increments (D) were an exponential function of hourly temperature (T): $\mathrm{D}=1/24\ (\mathrm{e}^{a-b\mathrm{T}})$, where values of *a* and *b* for the developmental stages of *P. ulmi* and *T. pyri* were empirically derived (Hardman, 1989; Hardman and Rogers, 1991). Although developmental increments were accumulated on an hourly basis, transfers of individuals to the next developmental stage (and all other process simulated in the model) occurred on a daily basis. If cumulative development was sufficient, individuals matured and moved to the first age class of the next developmental stage. At higher temperatures the developmental increment could be greater than one step in the 24-h interval, and transfers could be to Class 2 or 3 or higher. Other details of the *P. ulmi* model are given in Hardman (1989).

Stage-specific predation

To model mixed age class consumption we assumed that the prey biomass consumed by a predator was a function of the total biomass available and we based the functional response of predators on prey biomass. We will describe the relationships symbolically by considering only one predator age class. Let T be the total biomass consumed by a predator in a particular lifestage, B be the total biomass available for consumption, B_i be the biomass of prey stage i and N_i be the density of prey stage i. Then, $T=f(B)$ and $B=\sum B_iN_i$. Total consumption, T, by predators in a particular lifestage was determined by ($T=\sum C_iB_i$), where C_i is the number of prey of stage i consumed. We assumed that consumption of a particular prey lifestage was proportional to the product of its density and relative susceptibility to predation. Symbolically, $C_i=P_i\sum C_i$ where P_i is a proportionality factor defined as $N_iS_i/\sum(N_iS_i)$ and S_i is the relative susceptibility to predation of prey lifestage i. Susceptibility was determined relative to a standard of 1 for prey larvae. Consumption was first determined on a per predator basis for each predator lifestage. Consumption by all the predators in a lifestage was determined by multiplying consumption by the density of predators. Consumption of a particular prey lifestage was then summed over all predator lifestages. If consumption exceeded the available density, all consumption was scaled by the ratio of available prey to consumed prey.

Spatial distribution

The predation component of the model incorporates the spatial incongruity of *T. pyri* and *P. ulmi*. Populations of prey and predator do not mix uniformly; some predators are on leaves not occupied by prey and some prey are on leaves not occupied by predators. Field data (Nyrop, 1988) indicate that *T. pyri* and *P. ulmi* are randomly associated at the spatial scale of a leaf and at the scale of a leaf cluster. We incorporated spatial incongruity by considering only the zero terms of a joint probability distribution for prey and predator abundance on leaves, where the joint distribution was determined as the product of the zero terms of the marginal distributions of the two species. Counts of both species on leaves can be described by a negative binomial distribution with the variance (s^2) a power function of the mean (m) (Taylor, 1961), $s^2 = am^b$. For *T. pyri*, $a = 2.38$ and $b = 1.2$, and for *P. ulmi*, $a = 4.32$ and $b = 1.42$. Using the zero terms of the negative binomial distributions for *T. pyri* (P_{0t}) and *P. ulmi* (P_{0p}), we determined the density of *P. ulmi* that were available to be preyed upon and the density of predators available to attack prey. We determined mortality due to predation using the zero terms from the marginal distributions as follows: Let C_i be the average number of prey of life stage i consumed per leaf on leaves with prey and predators. The proportion of leaves with *T. pyri* and *P. ulmi* is $(1-P_{0t})(1-P_{0p})$. The total number of *P. ulmi* consumed is $K(1-P_{0t})(1-P_{0p})C_i$ and the total *P. ulmi* population is $K(N_i)$, where K is the total number of leaves and N_i is the density of a particular prey lifestage. The mortality rate of *P. ulmi* in lifestage i due to predation was then determined as $[K(1-P_{0t})(1-P_{0p})C_i]/[KN_i]$, or equivalently as $(1-P_{0t})(1-P_{0p})(C_i/N_i)$.

Estimating the predators' functional response

The functional response and the parameters B_i and S_i were estimated using data collected in laboratory experiments. Data were collected primarily using adult female predators because this lifestage, due to its voracity and longevity, is responsible for much of the predation that occurs. Predation rates were estimated using the following experimental design. Prey and a single predator were confined on the ventral side of an apple leaf that was in turn placed on a bed of wet cotton. The leaf was ringed with a sticky material to prevent prey and predator escape. Experimental units (leaves) were housed in environmental chambers at various temperatures, 70 RH and a 16:8 light:dark cycle. Consumption was determined at 24-h intervals and prey replenished. Predators originated from a laboratory colony. Each experimental unit was observed for 5–10 days and 5–10 experimental units were used in each experiment. Predation rates were calculated as the average number of prey consumed per day, and estimates of variation were based on between day variation.

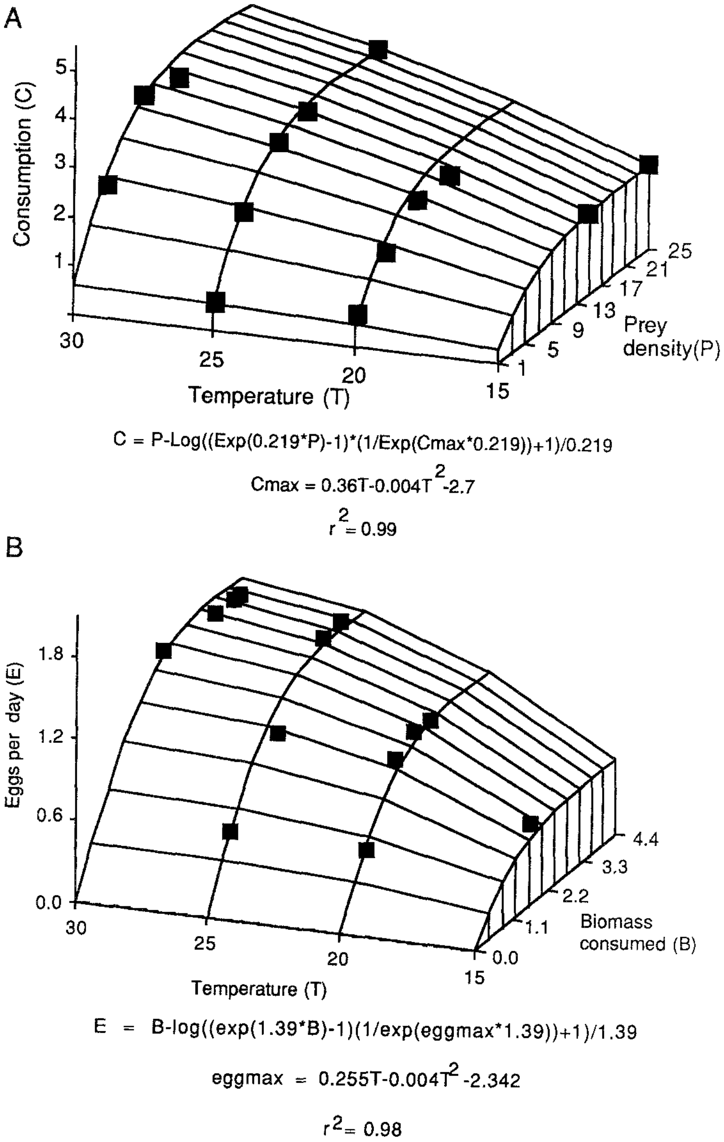
To parameterize a functional response model, predation of adult female *P. ulmi* by adult female *T. pyri* was estimated at 15, 20, 25 and 30°C and at prey densities ranging from 1 to 25 per leaf. Royama's (1971) predation function was fit to this data by first describing maximal predation as a function of temperature using a second order polynomial and then by fitting the overall equation to the data using nonlinear regression. The resulting model is shown in Fig. 4a. We assumed that the form of the functional response was similar for other predator life stages but proportionally reduced. From additional experiments, the following proportionality constants were obtained for other developmental stages of *T. pyri*: protonymphs, 0.2; deutonymphs, 0.4; preovipositional adult females, 0.9; and adult males, 0.4.

The relative biomass contributed by each prey life stage (B_i) was estimated as the maximal consumption of the life stage by adult female predators divided by the maximal consumption of *P. ulmi* adult females by adult female *T. pyri*. Biomass values based on these data after rounding were: larvae, 0.25; protonymph, 0.4; deutonymph, 0.6, adult female, 1.0, and adult male, 0.7. *Typhlodromus pyri* do not consume *P. ulmi* eggs.

Susceptibility to predation values (S_i) were required for each prey and predator lifestage. For adult female predators these were estimated as the ratio of consumption of a prey lifestage with respect to another prey lifestage. Consumption studies were done comparing consumption of adults to immature (protonymphs and deutonymphs), adults to larvae, and immatures to larvae. For other predator lifestages, values were determined subjectively. Estimates are shown in Table 1.

Two types of experiments were conducted to determine how well the predation model predicted consumption on the leaf arenas. First, consumption by a single female predator feeding on different densities of a single age class of prey was determined and compared with predicted values. This experiment checked the adequacy of the functional response model. Second, consumption by a single female predator feeding on different lifestages of prey was determined and compared with predicted values. This experiment checked the adequacy of the way in which we dealt with mixed age classes of prey. Results are shown in Table 2. We conclude that the predation component of the model is a reasonable representation of predation on the experimental arenas.

In the laboratory experiments we observed that *T. pyri* would feed on their own larvae and protonymphs but did not feed on eggs and if they did attack other life stages, it was infrequent. We also observed that in the presence of *P. ulmi*, *T. pyri* fed less frequently on their own immatures. Cannibalism was



$$C = P\text{-}\mathrm{Log}((\mathrm{Exp}(0.219*P)-1)*(1/\mathrm{Exp}(Cmax*0.219))+1)/0.219$$

$$Cmax = 0.36T-0.004T^2-2.7$$

$$r^2 = 0.99$$

$$E = B\text{-}\log((\exp(1.39*B)-1)(1/\exp(eggmax*1.39))+1)/1.39$$

$$eggmax = 0.255T-0.004T^2-2.342$$

$$r^2 = 0.98$$

Fig. 4. Response surfaces for adult *Typhlodromus pyri* based on laboratory experiments. (A) the functional response of *T. pyri* to variation in prey density and temperature and (B) the ovipositional response of *T. pyri* to variation in temperature and prey consumption.

incorporated into the model by including *T. pyri* larvae and protonymphs as prey items. We assumed they contributed the same amount of biomass as respective *P. ulmi* lifestages; however, the susceptibility of the immature *T. pyri* to predation was very low, with S_i values being 0.1 for larvae and proto-

TABLE 1

Relative susceptibility of a *P. ulmi* lifestage to predation by a *T. pyri* lifestage. A value of zero means a predator could not consume the prey lifestage

Prey	Predator				
	Larvae	Protonymph	Deutonymph	Adult female	Adult male
Egg	0	0	0	0	0
Larvae	0	1	1	1	1
Protonymph	0	1	1	1	1
Deutonymph	0	0.5	1	1	1
Adult female	0	0	0.5	0.7	0.5
Adult male	0	0.5	1	1	1

TABLE 2

Validation of the functional response model of adult female *Typhlodromus pyri* on *Panonychus ulmi*. Comparison of observed consumption rates by adult *T. pyri* of mixed age groups of *P. ulmi* adults, nymphs (protonymphs and deutonymphs) and larvae, with predictions of model. Consumption was measured at 24-h intervals and was based on observations of 7 to 10 predators observed for 3 to 5 days

P. ulmi density			Temp.	Consumption by predators					
				Observed			Predicted		
Adult	Nymph	Larva		Adult	Nymph	Larva	Adult	Nymph	Larva
2	2		25	0.53	1.40		0.66	1.76	
2	4		20	0.42	1.80		0.40	2.02	
5	5		30	1.41	3.12		1.40	3.20	
4	4	4	20	0.50	1.44	2.63	0.65	1.70	2.21
5	5	5	25	1.11	1.83	2.60	0.95	2.23	3.18

nymphs when attacked by deutonymph and adult female predators, and zero for all other predator lifestages.

Oviposition rates

Oviposition by *T. pyri* is influenced by temperature, age of the female, and food consumption. We collected data on oviposition in the same way that data was collected on predation. These data were fit to the same function used to model the functional response (Fig. 4b). To account for differences in oviposition due to age of the female, females were divided into 20 age classes with the proportions of maximal oviposition for every two age classes: 0.75, 1.0, 0.9, 0.65, 0.55, 0.35, 0.3, 0.25, 0.2, and 0.

Panonychus ulmi reproduction rates in the model depended on temperature and female age. They were also related to food quality, declining with the aging of leaves as the season progressed, and were density dependent, i.e., proportional to the accumulation of mite-days when these exceeded 800 per leaf. Details of and the empirical basis for these relationships are found in Hardman (1989) and Hardman and Rogers (1991).

Alternate food

Estimates of the contribution of alternate food to the reproductive success of *T. pyri* were derived from discussions in the literature (e.g. Chant, 1959; Dosse, 1961; Genini, 1987). Alternate food was included at four levels. Abundant alternate food allowed for a realization of 100% of ovipositional capacity regardless of *P. ulmi* consumption before 30 June and 35% of maximal oviposition if insufficient *P. ulmi* were consumed thereafter. (This was an approximation of Genini's (1987) conclusions about the pattern of availability of alternate food.) A moderate level of alternate food allowed for 50% of ovipositional potential prior to 30 June, and 10% after, low alternate food allowed for 25% of demand to be met before 30 June and 5% after, and the final level had no alternate food available at all.

In the simulations daily mean temperature was used to compute potential per capita demand for food (expressed as biomass units of adult female *P. ulmi*) by an ovipositing adult predator. Next, *T. pyri* on leaves with *P. ulmi* were considered separately from those on leaves lacking prey. On leaves with *P. ulmi*, the total food consumed by an ovipositing female was the sum of the per capita consumption of *P. ulmi* plus the fraction of demand that could be met by alternate food. On leaves with no *P. ulmi*, total food consumed was that fraction of demand that could be supplied by alternate food. In both cases, total food consumed and mean temperature were then used to compute per capita egg production.

Model validation

The ability of the model to simulate field population trends was tested by comparing observed *T. pyri* and *P. ulmi* densities in the Darrow and Crittendon orchards in 1986 and 1987 with model predictions. These sites and dates were selected because they were the only data sets with counts of eggs, immatures, and adults of both species. The model was initialized with the first density estimates of each year. Initial densities of immatures were equally divided among larvae, protonymphs, and deutonymphs. Daily maximum and minimum temperature data collected at Geneva, NY were used to drive the model. For the validation runs, alternate food was assumed to be at a moderate level.

Predicted and observed densities of egg and motile (immature plus adult) *T. pyri* and *P. ulmi* for the Darrow and Crittendon sites are shown in Figs. 5

and 6 respectively. The fit between predicted and observed dynamics of *T. pyri* and *P. ulmi* was poorer in 1986 than in 1987. At both sites, *P. ulmi* numbers in late July and early August were considerably higher than predicted while densities of *T. pyri* in June at the Darrow location and in July at Crittendon were less than the predicted values.

Two factors that could have depressed *T. pyri* densities are a lack of alternate food and additional mortality of predators caused by insecticide applications. These simulations were run with a moderate level of alternate food, but we know that abundance of apple rust mite actually varies a great deal from year to year. To test the hypothesis that a low level of alternate food in early 1986 could be responsible for the pattern, the simulations were repeated with no alternate prey (Figs. 5e,f and 6e,f). At the Crittendon site, the general pattern of dynamics was quite well represented by the model, although *P. ulmi* motiles and *T. pyri* egg and motiles peaked somewhat later than predicted, and *P. ulmi* egg densities were not quite as high as predicted. At the Darrow site, observed *P. ulmi* densities were still much higher than predicted. This discrepancy may have been due to immigration by *P. ulmi* and/or the presence of some organophosphate-susceptible *T. pyri*. In 1986 the densities of *P. ulmi* in trees adjacent to the sampled trees in Darrow were quite high (>90 motiles per leaf). It is very likely that immigration contributed to the population increase observed, although the magnitude of this factor would be difficult to assess. In later years densities of *P. ulmi* in surrounding trees were greatly reduced because of dispersal of *T. pyri*, and thus were unlikely to be as important (JPN, unpublished data). It is also possible that the insecticide applications may have had some impact on *T. pyri* numbers in the early years. The predators released at Darrow and Crittendon were assumed to be resistant to the insecticides used, but initially a proportion of the population may have been susceptible.

Despite considerable differences between predicted and observed dynamics in 1986, the model predicted regulation of the *P. ulmi* population and this did in fact occur. Thus, while the detailed prediction of dynamics in 1986 was not good, the regulatory influence of *T. pyri* was captured. By 1987 the fit between predicted and observed dynamics for both species was quite good for both sites. Based on these comparisons, we conclude that the model captures the essence of single-season *T. pyri*–*P. ulmi* dynamics on apple trees. Thus we use it here as a tool for exploring factors that might contribute to the persistence of the *T. pyri*–*P. ulmi* system.

Model dynamics

We used the model to explore the hypothesis that certain aspects of the *T. pyri*–*P. ulmi* interaction, and in particular the foraging behaviour of *T. pyri*, might help explain the dynamic patterns we saw in our field studies. We first

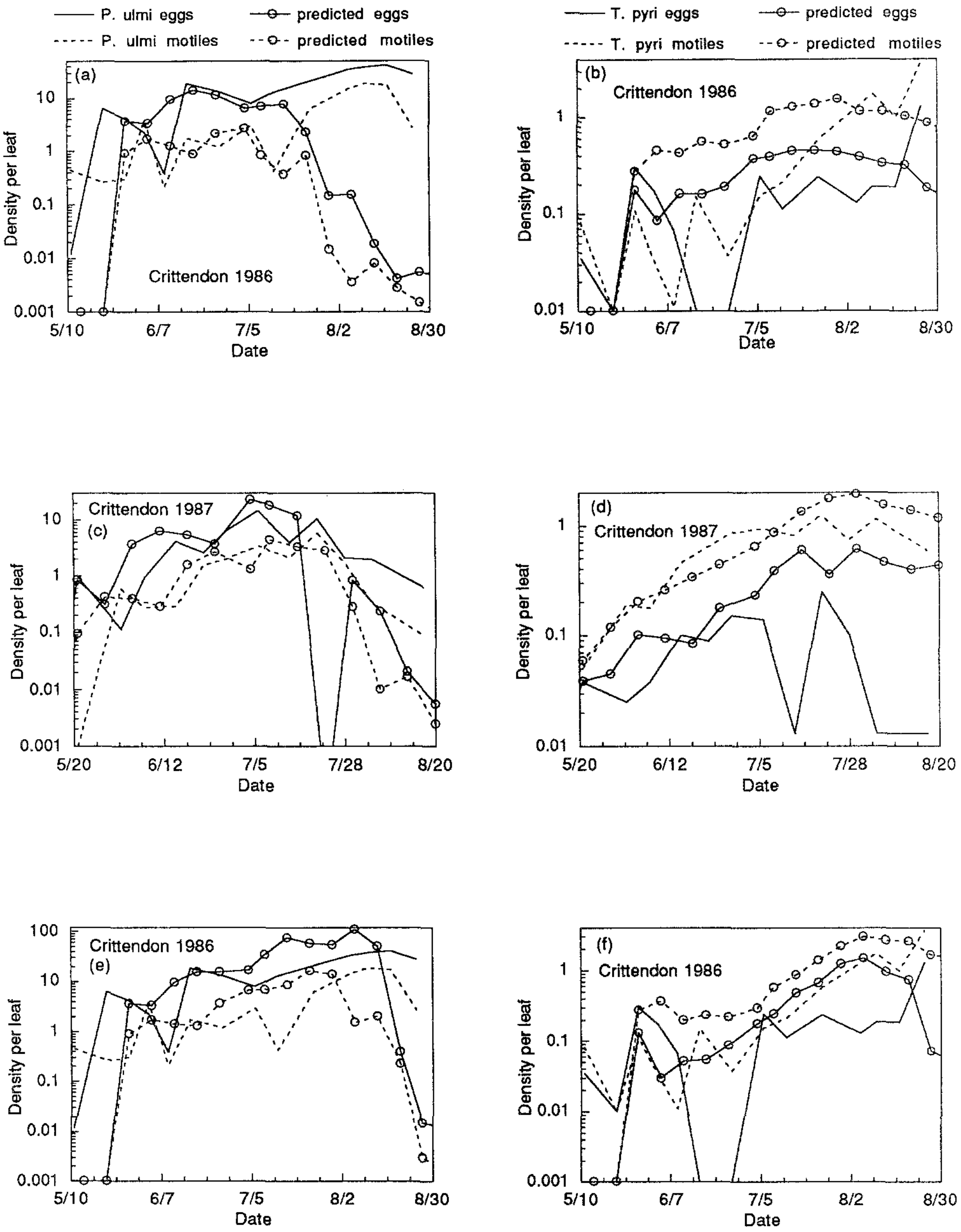


Fig. 5. Predicted and observed densities of *Panonychus ulmi* and *Typhlodromus pyri* eggs and motiles for New York orchard Crittendon in 1986 and 1987. Values predicted by the simulation model were obtained using moderate alternate food for (a) through (d) and no alternate food for (e) and (f).

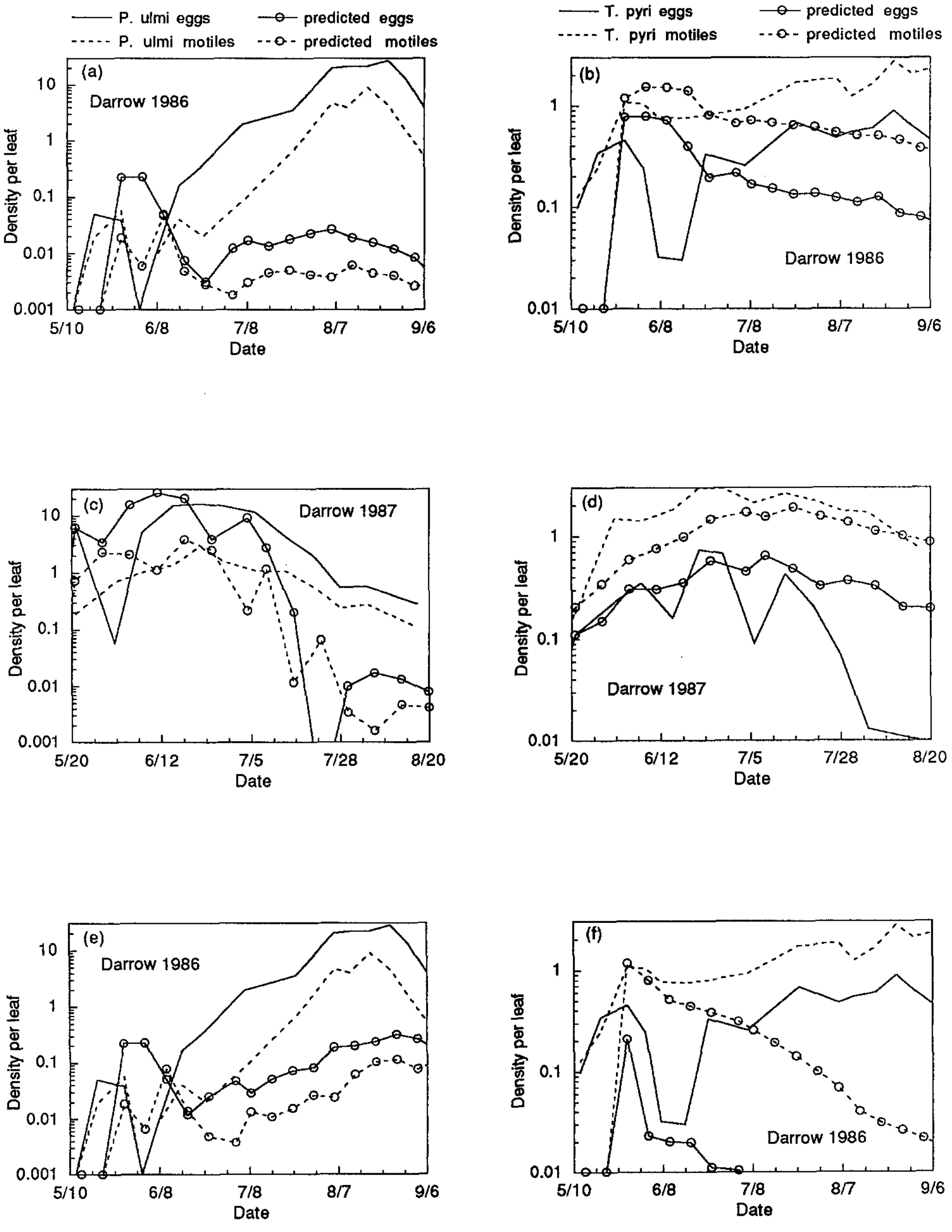


Fig. 6. Predicted and observed densities of *Panonychus ulmi* and *Typhlodromus pyri* eggs and motiles for New York orchard Darrow in 1986 and 1987. Values predicted by the simulation model were obtained using moderate alternate food for (a) through (d) and no alternate food for (e) and (f).

looked at the effect of initial densities, the presence of alternate food and cannibalism by *T. pyri* on the outcome of the predator–prey interaction within seasons. We then looked at how alternate food, overwintering mortality, cannibalism, and spatial congruity affected persistence of the system over a period of several years.

Unless specified, initial conditions (1 May) for all the simulations were the equivalent of 0.5 *P. ulmi* overwintering eggs per leaf and 0.01 *T. pyri* adult female per leaf. *Panonychus ulmi* eggs do not overwinter on leaves but on twigs and branches; however, densities per leaf were used to allow consistency with other density expressions. Temperature data used to drive these simulations were those recorded from March through October 1990 at Kentville, Nova Scotia.

Single-year dynamics

Initial densities. The ability of *T. pyri* to 'control' *P. ulmi* densities within one season was very sensitive to initial prey and predator densities (Fig. 7). Small changes in initial predator densities caused relatively large differences in the accumulation of mite-days through a season. The current cut-off point for successful biological control is ≤750 mite-days. In general cumulative mite-days declined exponentially with increasing predator density, although for an initial *P. ulmi* density of 5.0 overwintering eggs, the decline was not monotonic (Fig. 7). The initial increase in mite days over the lower range of *T. pyri* densities occurred because egg production in *P. ulmi* is density dependent. The slightly higher initial predator density limited *P. ulmi* densities early in the year, resulting in higher summer egg production in early August, and thus a large increase in numbers of *P. ulmi* motiles late in the year.

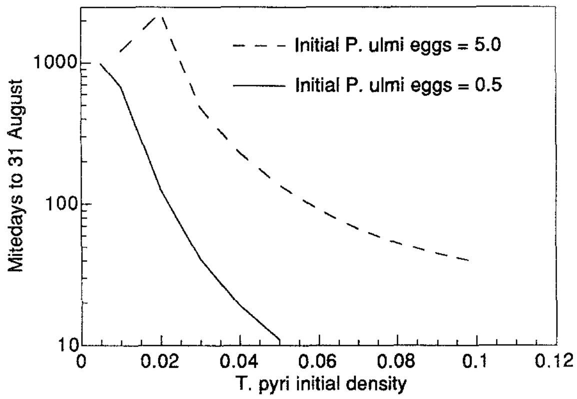


Fig. 7. Effect of initial density of *Typhlodromus pyri* and *Panonychus ulmi* on cumulative mite-days to 31 August, as predicted by the simulation model. Mite-days are the integral of motile *P. ulmi* density per leaf through time.

Thus both the absolute and relative initial densities of *T. pyri* and *P. ulmi* are critical in determining the pattern of within season dynamics. This suggests that factors that influence these densities, including relative overwintering mortalities and availability of alternate food early in the year might be expected to be of major significance.

Alternate food. With moderate or no alternate food, *T pyri* failed to regulate *P. ulmi* at an acceptable (≤ 750 mite-days) level when initial densities were 0.5 *P. ulmi* and 0.01 *T. pyri* (Fig. 8). With abundant alternate prey, biological control occurred. This pattern is probably due to the relatively weak numerical response of *T. pyri* coupled with the spatial incongruity of the prey and predator. At low prey densities *T. pyri* populations do not increase without alternate prey because a significant portion of the prey population goes undetected by the predator. When the prey population does begin to increase, *T. pyri* do not respond fast enough numerically to inhibit the prey's population growth. Availability of alternate prey and initial predator densities interact to affect biological control.

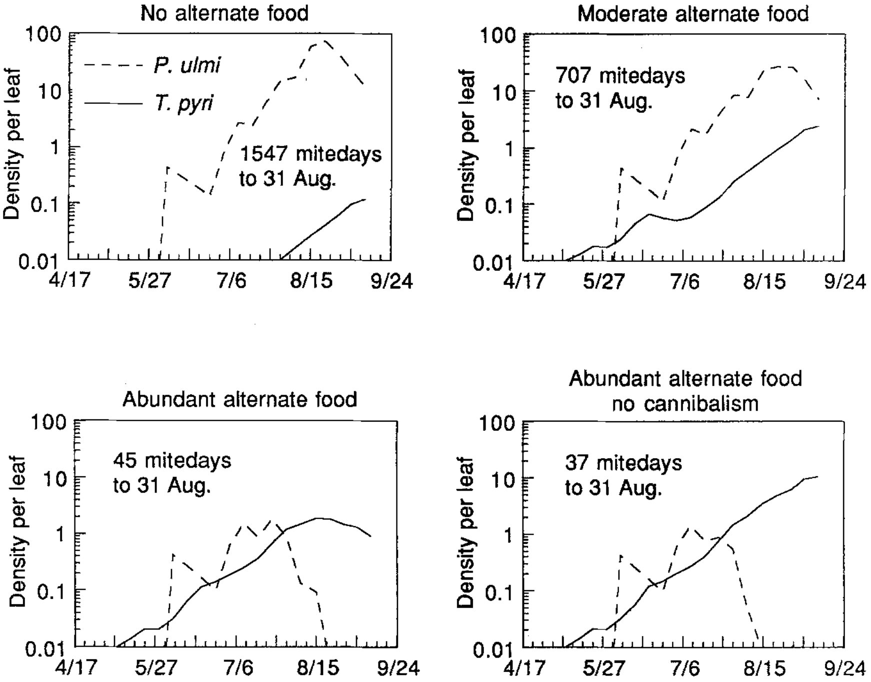


Fig. 8. Effect of varying level of alternative food and cannibalism on predicted within season dynamics of *Panonychus ulmi* and *Typhlodromus pyri*. Simulations (a) through (c) assume normal levels of cannibalistic behaviour by *T. pyri*, (d) assumes no cannibalism. Initial densities were 0.5 *P. ulmi* eggs and 0.01 *T. pyri* adult females.

Cannibalism. The effect of cannibalistic behaviour by *T. pyri* on seasonal dynamics was examined by removing this behaviour from the model under conditions of abundant food (Fig. 8d). Biological control was realized regardless of whether *T. pyri* was assumed to be cannibalistic. However, without cannibalism unrealistically high *T. pyri* densities occurred; we have never observed predator densities of 12 per leaf in apple orchards (Fig. 8d). Interestingly, the dynamics of the prey were not greatly changed when cannibalism was omitted. Cannibalism thus appears to be a significant aspect of the *T. pyri–P. ulmi* interaction in terms of determining densities, but does not seem to have an effect on the qualitative pattern of the dynamics of either species.

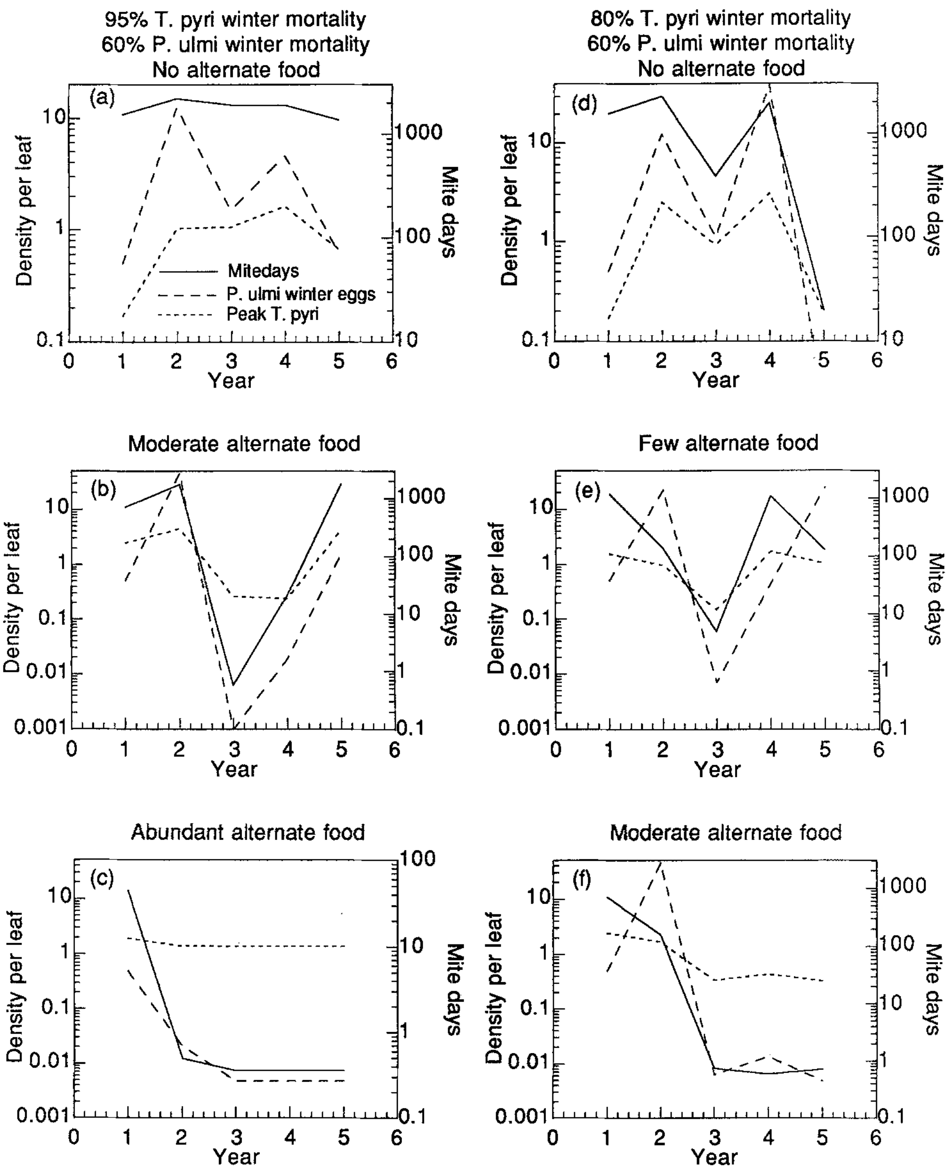
Multiple-year dynamics

The above simulations demonstrated that with appropriate initial densities and alternate food, *T. pyri* can regulate *P. ulmi* to economically acceptable levels, below 750 mite-days, within a single season. However, as we noted above, the observed dynamics are very sensitive to initial densities. Thus we now look at multiple-year dynamics to determine whether the biological characteristics of the *T. pyri–P. ulmi* interactions that we have identified as potentially significant influence the longer-term persistence of the two species.

All simulations began with initial conditions of 0.5 *P. ulmi* overwintering eggs and 0.01 *T. pyri* adult females. The model was run for 5 or 6 years, the time frame for which we have field data, with the same temperature pattern each year (data from Kentville, N.S., 1990). We were looking for evidence of persistence at low densities versus extinction, under different assumptions about overwintering mortality, availability of alternate food, cannibalism rate and spatial congruity of predator and prey.

Factors affecting initial density – overwintering mortality and alternate food. *Typhlodromus pyri* and *P. ulmi* have differential overwintering mortalities, with the predators generally suffering greater losses. Parent and Pilon (1978) in Quebec found that over a period of 8 years the percentage of mortality of winter eggs of *P. ulmi* varied from 44 to 71%. Factors responsible for this mortality were snow and ice of winter and predation in the spring and fall. Bohm (1960) in Austria noted that overwintering mortality of *T. pyri* varied from a typical value of 60% to a high of 92% in 1956 when a cold winter was followed by strong spring frosts. Chant's (1959) estimate of 97% mortality of *T. pyri* in the winter of 1954–55 in southeast England was obtained by comparing mites per leaf in October 1954 with the count in May of 1955. His general impression was that the winter mortality of phytoseids was high, probably 80 to 90%.

In the model, we assumed that overwintering mortality of *T. pyri* could vary from a low of 80% to a high of 95%, while *P. ulmi* suffered losses of 60%. Both overwintering mortality and the availability of alternate food affect den-


95% T. pyri winter mortality
60% P. ulmi winter mortality
No alternate food

80% T. pyri winter mortality
60% P. ulmi winter mortality
No alternate food

Moderate alternate food

Few alternate food

Abundant alternate food

Moderate alternate food

Fig. 9. Effect of winter mortality of *Typhlodromus pyri* and level of alternate food on predicted multiple year dynamics of *Panonychus ulmi* and *T. pyri*. Simulations (a) through (c) assume 95% winter mortality, while (d) through (f) assume 80% winter mortality of *T. pyri*. All simulations include normal levels of cannibalism. Mite-days are to 31 August.

sities at the beginning of the season, and might be expected to interact, either in a compensatory or additive fashion. We thus consider the two factors jointly, with varying levels of alternate food as defined earlier.

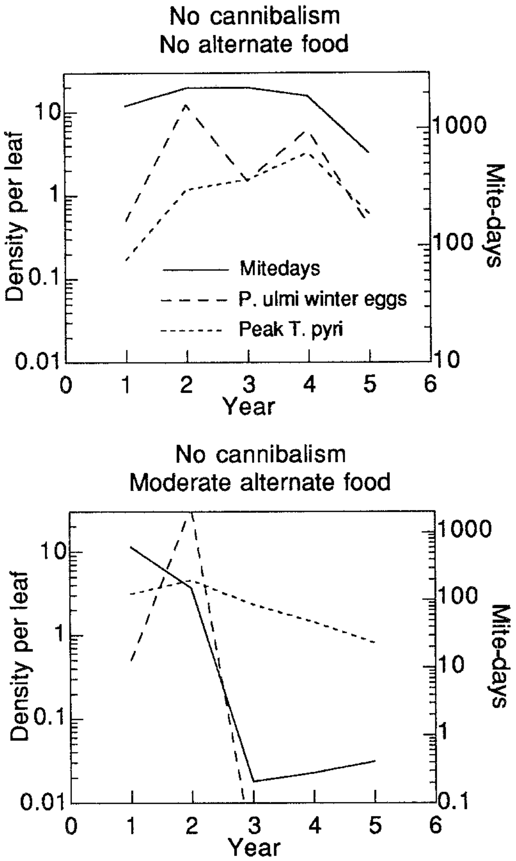


Fig. 10. Effect of removing cannibalistic behaviour from the simulation model under two levels of alternate food on predicted multiple year dynamics of *Typhlodromus pyri* and *Panonychus ulmi*. Mite-days are to 31 August.

At very high levels of predator mortality (95%), the importance of alternate food in the control of *P. ulmi* is clear (Fig. 9a–9c). When no alternate food was available biological control did not occur during any of the five years of simulation, with cumulative mite-days always exceeding 1300. With moderate levels of alternate food, biological control occurred in the first, third and fourth years; however, predators failed to suppress *P. ulmi* in the second and fifth years. The pattern is suggestive of oscillations, and the predicted density of *P. ulmi* overwintering eggs is very near zero one year. When alternate food was abundant, biological control occurred each year, *P. ulmi* were regulated to very low numbers, and *T. pyri* were relatively abundant. This pattern is similar to our field data from New York (Fig. 2).

The general pattern remained similar at lower levels of predator overwintering mortality (80%) when availability of alternate food was varied from

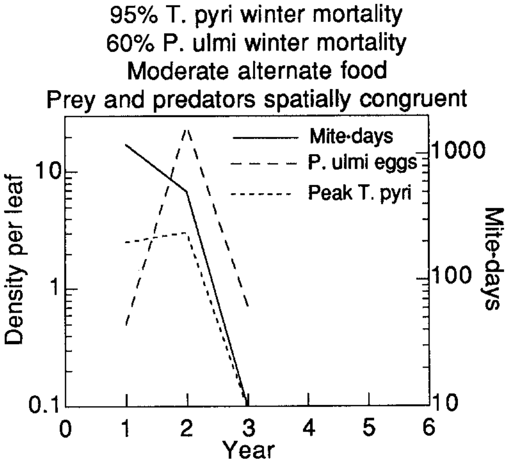


Fig. 11. Effect of removing spatial incongruity between predator and prey from the simulation model on predicted multiple year dynamics of *Typhlodromus pyri* and *Panonychus ulmi*. Mite-days are to 31 August.

zero to moderate (Fig. 9d–9f). With lower predator overwintering mortality and no alternate food there was a suggestion of oscillations between years of effective and ineffective biological control (Fig. 9d), not unsimilar to the pattern generated by high mortality and moderate food (Fig. 9b). As the level of alternate food was increased, control was seen over greater periods of time. With moderate alternate food (Fig. 9f), the pattern was very similar to that seen with abundant food and higher predator mortality (Fig. 9c).

Cannibalism. A process that might be expected to act as a damping factor, or negative feedback on predator population growth, is cannibalistic behaviour by *T. pyri*. In single-season dynamics, cannibalism appeared necessary to produce realistic predator densities (Fig. 8d). Here we look at the effect of cannibalism on multiple-year dynamics. *Typhlodromus pyri* overwintering mortality was set to 95% and *P. ulmi* overwintering mortality was kept at 60%, and the level of alternate food at either zero or moderate. From these simulations, cannibalism by *T. pyri* appears to be detrimental to control of *P. ulmi* (compare Fig. 10 with Fig. 9a and 9b). Removing cannibalism from the predator–prey interaction resulted in lower accumulated mite-days and lower densities of overwintering eggs. Without cannibalism, a persistent low density system was realized with a moderate level of alternate food (Fig. 10b), while with cannibalistic predators and the same parameter combinations *P. ulmi* densities were not held below the cutoff of 750 mite days (Fig. 9b).

Spatial congruity. Finally, we evaluated the importance of including a spatial component in the model. Incongruity between the prey and predator was eliminated by assuming uniform mixing of the two populations, eliminating the spatial component of the predation model. Not unexpectedly, this component was of over-riding importance; without spatial incongruity *P. ulmi* became extinct (Fig. 11). (We assumed extinction occurred if densities fell below 0.0001.) *Typhlodromus pyri*, however, persisted, but at very low densities (0.028 per leaf in the third year).

DISCUSSION

Debates about the stability or persistence of predator–prey interactions, or of predator and prey populations in biological control systems are sometimes cast in terms of a dichotomy: there is either persistence or extinction. The debate, however, cannot be separated from issues of spatial scale, since the perceived stability (persistence) of an interaction or population is very much a function of the spatial scale under consideration. Thus, instead of attempting to classify our system as persistent or not, in this study we have attempted to look at how the degree of persistence (as we have defined it) changes as we move across spatial scales. What we found was that at the larger spatial scale, that of an orchard, both species appeared to be persistent, at least over the time frame that we used. As we moved to a smaller spatial scale, that of a tree, we found a lower degree of persistence, which, on the surface should not have been surprising. What was novel about these results was that the degree of persistence did not appear to change at the same rate for both predator and prey, that is, *P. ulmi* seemed to be less persistent than *T. pyri*.

This dynamic pattern is particularly note-worthy since it occurred in a biological control system, where the predator has been demonstrated to exert significant control on its prey. One might expect to find nearly any pattern where a predator is not closely linked with its prey, but the *T. pyri–P. ulmi* interaction is strongly linked from the perspective of control. We argue that these dynamics emerge because certain aspects of the biology or behaviour of these two species cause the predator–prey interaction to be partially uncoupled, despite which, control of the prey is maintained. These behaviours are a generalist food habit, cannibalism and the tendency to have a non-congruent spatial distribution.

It is probably a rare biological control system where the predator and/or prey are completely confined to interacting with only the other species of the pair; generally the prey has other predators or parasites and the predator has other sources of food. Although at least some literature reviews have failed to support the view (Chung-lo, 1958), it has been and is still argued that most biological control agents have restricted host ranges, and that generalist predators or parasites are seldom effective (Greathead, 1986). Presumably, specialists are expected to show stronger numerical and functional responses to increases in the density of their prey and thus be better able to regulate them.

Thus *T. pyri* stands as something of an exception, it is effective despite, or as we will later argue, in part because of its generalist food habit.

Typhlodromus pyri is certainly a generalist predator. When *P. ulmi* are scarce *T. pyri* can survive and, in some cases reproduce, using alternate food sources such as mildew (Chant, 1959), pollen (Dosse, 1961), eggs and motile stages of two-spotted spider mite (Herbert, 1956), eriophyid mites (e.g. *Aculus schlechtendali* Nalepa) (Chant, 1959; Herbert and Sanford, 1969) and tydeid mites (Calis et al., 1988), all of which occur in apple orchards in New York and Nova Scotia. Chant (1959) also concluded that *T. pyri* feed on juices of apple leaves.

Although most mathematical theory pertaining to biological control has been developed for one predator (parasitoid)–one prey (host) systems (e.g. Hassell, 1978), stable interactions are certainly possible for models constructed with generalist predators (e.g. Hassell and May, 1986). The assumptions of Hassell and May's model resemble some of those in our model: use of the negative binomial to describe encounters between predator and prey, a Type II functional response and a numerical response by the predator to increases in prey density. Stability comes from three sources. First, the predator's dynamics are partially uncoupled from those of the prey, meaning that a prey crash doesn't necessarily lead to a predator crash. Secondly, spatial heterogeneity produced by the use of the negative binomial contributes to stability. Finally a rapid numerical response maintains the prey at low numbers. A fast numerical response could be the result of rapid reproduction by the predator in comparison with the prey or of 'switching' (Murdoch, 1969) from other food to the prey when densities increase (Hassell and May, 1986).

At least part of the cause of the dynamic patterns we observed can be found in the biological correlates of these three factors in the *T. pyri–P. ulmi* system. The generalist food habit enhances the persistence of the predator population, since a drastic drop in *P. ulmi* density does not necessarily cause extinction of the predator. In the New York orchards *P. ulmi* was absent, or nearly so, from some trees. while *T. pyri* persisted, and in the experiments in Nova Scotia the proportion of populations that were apparently extinct was considerably higher for *P. ulmi* than for *T. pyri*. Generalist feeding may explain the greater persistence of the *T. pyri–P. ulmi* system as compared with *P. persimilis–T. urticae. Phytoseiulus persimilis* is a more specialized predator that cannot reproduce in the absence of its primary prey, and is known for driving its prey extinct, at least in greenhouse situations (e.g. Chant, 1961). Successful and persistent biological control by *T. pyri* may be possible despite local extinction of *P. ulmi*, because the predator does not go extinct and thus is still present when trees are recolonized by *P. ulmi*.

Secondly, it appears that in contrast to being a detriment to successful biological control, the generalist food habit may be what allows *T. pyri* to be an effective control agent. It has been shown, both in our simulations here, and in at least one greenhouse experiment (Collyer, 1964) that the presence of alternate food such as the rust mite, actually enhances control of *P. ulmi* by *T. pyri*. Successful control requires that *T. pyri* not only be present when *P. ulmi* is present but also be capable of a rapid numerical response to increases in *P. ulmi* density. By itself, *T. pyri* has a weak numerical response. The development time of *T. pyri* is similar to *P. ulmi* but its fecundity lower (Herbert, 1961, 1962, 1981), and thus reproductive effort alone may not result in a numerical response sufficient for control. Presence of alternate food such as apple rust mite early in the season allows predator populations to build to greater densities before the major seasonal population increase of *P. ulmi*, increasing their impact on the target prey. In addition, studies have shown that *P. ulmi* is the preferred prey (Dicke, 1988; Dicke and DeJong, 1988), despite the fact that development and reproductive success is higher on apple rust mite (Dicke et al., 1990). Switching to a preferred prey as its density increases is another way of increasing a numerical response, and although it has not yet been demonstrated that *T. pyri* switches to *P. ulmi* when densities increase, it has been shown that for some as yet not understood reason, the rate of success of attack on *P. ulmi* actually increases in the presence of apple rust mite (Dicke et al., 1989).

The third factor in the stability of this system appears to be the spatial incongruity between the predator and prey. This should be a negative feature in a biological control system from the point of control, since increases in spatial incongruity increases the equilibrium density of the prey (Murdoch, 1989). In our simulations, we found the assumption of spatial incongruity between predator and prey to be absolutely essential to persistence of the predator–prey system. Without the spatial component, *P. ulmi* was driven extinct. In the presence of alternate food, *T. pyri* could persist, but at very low levels. We don't argue that this factor is necessary for successful control, but to the extent that it is present, it should enhance the persistence of *P. ulmi* at smaller spatial scales than that of an orchard. Spatial incongruity of *T. pyri* and *P. ulmi* in the field is present at the scale of leaves or leaf clusters (Nyrop, 1988). As the universe of leaves increases, we should expect to see increases in the persistence of the *P. ulmi* populations. The higher level of persistence of *P. ulmi* in the New York as compared with Nova Scotia orchards fits with this hypothesis. The New York trees were 12 years old in 1990, compared with 1 to 2 years in the Nova Scotia experiment. Even at the end of the second year, the size of one of the experimental trees was no larger than a branch on a mature full-size tree, and thus the number of leaf clusters or spatial complexity of an experimental tree was much less.

Cannibalism is probably widespread among phytoseids, as indicated by the general recommendation that phytoseid cultures be maintained as same-aged cohorts to avoid intraspecific predation (Overmeer, 1985). We (JPN, unpublished data) have observed *T. pyri* adults and deutonymphs preying on larvae and protonymphs in laboratory experiments. Clements and Harmsen (1990) also observed cannibalism in the lab in *Typhlodromus caudiglans* (Schuster). Adult *Phytoseiulus persimilis* and *Amblyseius degenerans* (Berlese) are also known to feed on both eggs and the immature motile stages of their own species (Yao, 1986).

We included cannibalism in our consideration of the *T. pyri–P.ulmi* interaction since this behaviour is known theoretically to have various effects on the dynamics of populations. It can behave as a negative feedback mechanism, adding to the stability of the system (Fox, 1975). On the other hand it can act as a time-lag in the density-dependent response of a population, particularly if the eaten and eaters are distinctly different age classes, potentially causing oscillatory behaviour in populations (Hastings, 1987: Orr et al., 1990). In our simulation, cannibalism as modelled had little effect on the dynamics of the interaction between *P. ulmi* and *T. pyri*. The inclusion of this behaviour was deemed necessary to obtain realistic predator densities, but the pattern of the dynamics was not dramatically changed. Not surprisingly, cannibalism tended to interfere with control of *P. ulmi*, resulting in higher levels of cumulative mite-days. However, as a negative feedback factor, cannibalism was not strong enough to allow for persistence of *P. ulmi* in the absence of spatial incongruity (Fig. 11).

In this paper we have looked at factors that we thought likely to impact the persistence of *T. pyri* and *P. ulmi*, as well as those likely to impact the effectiveness of the control exerted by *T. pyri*. We conclude that the persistence of *T. pyri* at the spatial scale of a tree is likely due to its generalist food habit and the presence of alternate food. This factor does not contribute to the persistence of *P. ulmi*, in fact high levels of alternate food tend to drive *P. ulmi* to very low densities, densities which in the real world could occasionally easily reach zero. The factor that tends to contribute most to the persistence of *P. ulmi* at this spatial scale is the spatial incongruity of predator and prey. Persistence of both predator and prey is not equivalent to biological control in this system. Some of the factors that contribute to low densities of *P. ulmi* (alternate food) contribute to the persistence of the predator but not the prey, while others (absence of cannibalism, spatial congruity) do not enhance the persistence of either. Thus, in sum, we have a system where control of the prey is generally effective, and at smaller spatial scales, the predator tends to be more persistent than the prey.

In this analysis of single populations, we do not claim to have completely explored the nature of the *T. pyri–P. ulmi* interaction. We have not allowed the alternate food, e.g. *A. schlechtendali*, to have its own dynamics. In addition, we know from our field data that immigration or movement of mites between trees probably plays an important role in the observed dynamics; in Nova Scotia the extent to which *T. pyri* could depress *P. ulmi* densities was affected by the immigration, and in New York, 'too high' densities of *P. ulmi* in the early years could most easily be explained by the proximity of heavily infested neighbouring trees. Thus the logical next step should probably be to expand the spatial context of the model to include a metapopulation structure, and to look at the effect of generalist feeding, within-population spatial incongruity and cannibalism on dynamics. The ultimate test of our hypothesis would, of course, be to manipulate these factors in a field situation to determine how they actually impact the predator–prey interaction.

ACKNOWLEDGEMENTS

This work was supported by NSERC Canada operating grants to SJW and grants by the New York Apple Research Association and New York Department of Agriculture and Markets to JPN.

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