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PATCH DYNAMICS OF A PHYTOPHAGOUS MITE POPULATION: EFFECT OF NUMBER OF SUBPOPULATIONS¹

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Abstract. I conducted a field test of the hypothesis that the dynamics of a predator–prey interaction should be affected by the number of interacting subpopulations within an assemblage. I used a “successful” biological control system, the phytophagous European red mite (*Panonychus ulmi*) and its predator, the phytoseiid mite *Typhlodromus pyri*. An orchard was established where apple trees were arranged in groups of 1, 4, or 16 and the dynamics of the mite populations on the trees followed over a season. The pests reached highest densities and were most persistent on trees in the largest groups. These results are explained in terms of an interaction between prey immigration/emigration and predation.

Key words: *biological control; dispersal; patch; phytophagous mites; population dynamics; predator–prey; temporal variability.*

INTRODUCTION

Classical biological control, the sustained suppression of a pest by an introduced predator or parasite, is usually thought to involve the presence of a stable equilibrium between the pest and natural enemy (e.g., Waage and Hassell 1984), perhaps produced by aggregative behavior on the part of the natural enemy (Beddington et al. 1978). Recently it has been suggested that an alternative source of stability might be dispersal on a larger spatial scale, linking partially isolated subgroups within a population (Murdoch et al. 1984, Reeve 1988). That dispersal between patches could allow predators and prey to coexist was suggested as early as the 1950s by Andrewartha and Birch (1954), and confirmed in the laboratory (Huffaker 1958, Pimentel et al. 1963). Huffaker (1958) showed that a phytophagous–predaceous mite system could persist for a number of generations provided there were sufficient numbers of habitat units (oranges) and these were arranged so as to inhibit predator dispersal more than prey dispersal. A similar set of laboratory experiments with houseflies, blowflies, and the parasitic wasp *Nasonia* resulted in the same conclusions (Pimentel et al. 1963). Since that time others have obtained qualitatively similar results in laboratory and greenhouse experiments (Takafuji 1977, Maly 1978) as well as models (e.g., Vandermeer 1973, Roff 1974, Hastings 1977, Crowley 1981, Morrison and Barbosa 1987, Nachman 1987a, b, Sabelis and Diekman 1988).

These laboratory modelling results raise the obvious question of the relevance of these types of dynamics to field populations; the evidence that has been presented to date is ambiguous at best (Taylor 1990). In this study I begin to examine this question for one case

of biological control, the control of phytophagous mites on apple trees by phytoseiid mites. Patch dynamics have frequently been invoked as possible contributors to stability for phytophagous mites and their predators (Helle and Sabelis 1985). I use field populations of the European red mite *Panonychus ulmi* (Koch) (Acarina: Tetranychidae), and its chief predator in the region, *Typhlodromus pyri* Scheuten (Acarina: Phytoseiidae) to test the hypothesis that pest population dynamics are affected by the number of closely linked subpopulations within an area.

European red mite (ERM) first became a problem in eastern Canada in the 1930s with the extensive use of sulphur fungicides, and densities of the pest subsequently exploded in the 1950s with the use of broad-spectrum pesticides (Pickett 1959, MacPhee and Paradis 1981). Under conditions of low or no pesticide use, European red mite (ERM) abundances remain low, and this control has frequently been attributed primarily to the phytoseiid mite, *T. pyri* (Collyer 1980, Cranham and Solomon 1981, Gruys 1982, Zacharda 1989). This system thus constitutes a case of “successful” biological control. Although there is a considerable body of information on the biology of both species (e.g., MacPhee 1961, Herbert 1970, 1981, Putman 1970, Herbert and Butler 1975), the mechanisms by which *T. pyri* controls the pest are not yet clear. Here I test the hypothesis that the mechanisms underlying control might be related to the spatial arrangement or heterogeneity of the environment. I address the question: How does changing the spatial dynamics of a predator–prey interaction affect the temporal dynamics of the system?

STUDY ORGANISMS

European red mite

European red mite is considered an important pest of apple and other deciduous fruit trees, and the first recording in Nova Scotia was in 1911 (Gilliatt 1935).

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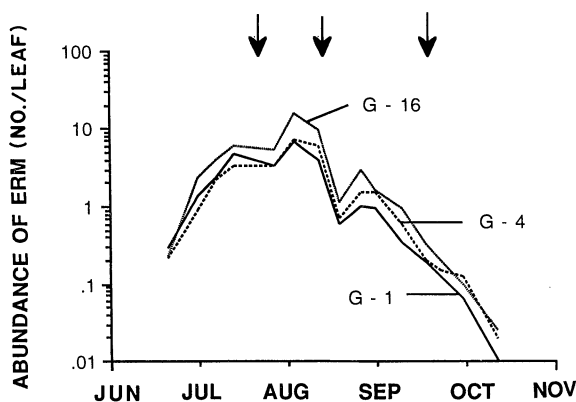


FIG. 1. Change in abundance of European red mite (ERM, *Panonychus ulmi*) over the season as determined by weekly field counts on 51 target trees. The three treatments were group sizes of: 1 (G-1), 4 (G-4), and 16 (G-16) trees. Arrows indicate dates when all 179 trees were sampled and ERM identified to stage.

ERM damages apple trees by feeding on the leaves, reducing transpiration, chlorophyll levels, and net photosynthetic rates (Mobley and Marini 1990), resulting in lower production of apples. ERM passes through 3–5 generations per season in the study area (Herbert 1970). The first generations lay summer eggs on the leaves, while the last produces overwintering eggs that are laid in crevices on the bark. ERM has five principal life stages: egg, larva, protonymph, deutonymph, and adult, with each motile stage entering a quiescent, non-feeding stage prior to molting. Adult females are responsible for almost all the intertree dispersal within an orchard. Although dispersal is by wind, under particular temperature, humidity, and wind conditions, the mites display behavior that increase the likelihood of being carried away by the wind (Johnson and Wellington 1984).

Typhlodromus pyri

T. pyri is a common phytoseiid predator of ERM in eastern Canada and the northeastern United States. It can feed on pollen and fungi, as well as other mites such as *Aculus schlechtendali* (Nalepa) and *Tetranychus urticae* Koch, but both behavioral and diet analysis have shown that ERM is the preferred prey (Dicke 1988, Dicke and DeJong 1988, Nyrop 1988). Kairomones seem to be involved in local search behavior and longer range dispersal appears to be by wind (Sabelis and Dicke 1985).

METHODS

I varied the spatial arrangement of apple trees in an orchard to manipulate the immigration/emigration rate of both predator and prey. Trees were planted in groups of three sizes: 1, 4 (2×2), or 16 (4×4) trees per group. Within groups, trees were 2 m apart (far enough to preclude among-tree competition for water or nu-

trients at this stage), and groups were separated by a minimum of 20 m. Eight groups each of 4 and 16 trees (G-4 and G-16), and 19 single trees (G-1) were planted in a stratified random design. The experimental plots were planted in early May 1989, using 1-yr-old whips of a scab-resistant MacIntosh derivative, Nova-Mac, in a pasture located in the Annapolis Valley of southwestern Nova Scotia, Canada. Trees already contained some overwintering stages of ERM and *T. pyri*, and ERM populations were augmented in late May by attaching randomly selected infested leaves to the trees. The ground was kept clear of weeds to a radius of 50–75 cm, and the surrounding pasture kept closely mowed to a radius of 2 m. The remainder of the pasture was mowed twice during the season. No insecticides or fungicides were applied to the trees or surrounding area.

ERM densities were monitored approximately weekly from June through October on all single trees, and on two trees from each of the larger groups (51 “target” trees in all). In groups of 16, the target trees were always located in the center of the block. Ten leaves per tree were examined for ERM using hand lenses ($5 \times$ magnification) in the field, as the trees were too small to allow weekly samples of leaves to be removed from the trees. Mites could not be reliably assigned to stage using this method. To augment these censuses, on three occasions through the season (July, August, September), samples of 5–7 leaves were removed from each of the trees in the orchard and examined in the laboratory (179 trees in all). ERM and *T. pyri* were counted and separated by stage (egg, larva, protonymph, deutonymph, quiescent, mature female, mature male).

Dispersal was monitored using 100-cm² sticky cards placed at midtree height and 75 cm distance from the trees. Four cards were placed around each of the target trees, and for the groups of 16, an additional card was placed on each side of the whole block. Cards were put out on three dates and left for varying lengths of time: 30 June (14 d), 13 July (30 d), 23 August (40 d).

ANALYSES

Data were subjected to analysis of variance or regression as described below. Appropriate transformations were selected based on two criteria: normality, using the Kolmogorov-Smirnov test, as modified by Lilliefors (1967), and Bartlett’s test for homogeneity of variance. In each case, logarithmic, square-root, and fourth-root transformations were tested.

RESULTS

The prey

Density of ERM.—Both the weekly field counts (Fig. 1) and the laboratory counts (Fig. 2) indicated that ERM was more abundant on trees in groups of 16 than on single trees or those in groups of 4.

Weekly field counts per tree were used to calculate cumulative mite-days per tree as: $\sum 0.5(N_{x+1} -$

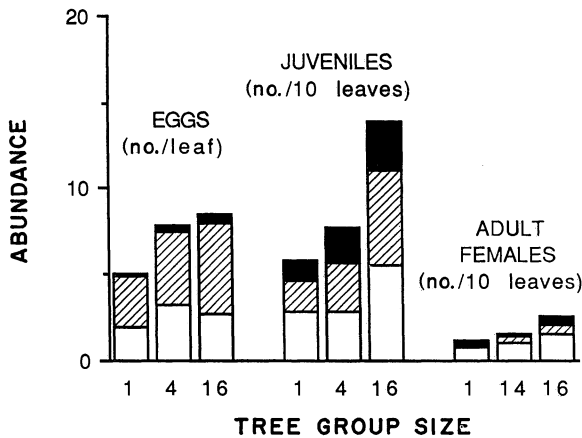


FIG. 2. Effect of tree group size on abundance of European red mite (*Panonychus ulmi*) by stage: eggs, juveniles (larvae, protonymphs, deutonymphs, quiescents) and adult females. Means across trees are shown for July (hollow bars), August (hatched bars) and September (solid bars). Significant effects of group size ($P < .05$) were seen for juvenile ERM.

$N_x)D_{x+1,x}$, where N_x is the number of ERM per leaf on sampling date x , and $D_{x+1,x}$ is the number of days between sampling dates (Hull and Beers 1990). G-16 trees had significantly more mite-days than G-1 or G-4 trees ($P = .007$). The cumulative number of mite-days were: 245 ± 42 , 211 ± 40 , and 396 ± 53 for G-1, G-4, and G-16 trees, respectively (mean \pm 1 SE).

Analysis of the counts conducted on all trees on three dates yielded qualitatively similar results. Counts for eggs, juveniles (larvae, nymphs, and quiescents), and adult females were fourth-root transformed and subjected to repeated-measures analysis of variance. Juveniles were more abundant on G-16 trees than in the smaller groups ($P = .02$), but there was no significant effect of group size on number of eggs ($P = .24$) or adult females ($P = .13$) (Fig. 2).

Densities of ERM did not reach particularly high levels in this orchard. The highest average counts per tree were much lower than the peak counts of 100 plus motile ERM per leaf commonly seen in orchards under a standard chemical control regime (Parent 1967, Hardman and Gaul 1990). Cumulative mite-days were also considerably lower than the level at which economic injury has been shown to occur (1250 mite-days: Hull and Beers 1990).

Age structure of ERM.—The age structure of the populations differed significantly among groups in August (near peak summer densities) (Table 1). G-16 trees had a significantly lower proportion (84 vs. 91 and 93%) of their populations at the egg stage ($P = .003$), and a higher proportion in the juvenile motile stages (14 vs. 7 and 5% for G-4 and G-1 trees; $P = .006$). Age structure did not vary significantly among group sizes in the July or September samples, when average percentages of eggs and motile stages were 81 and 9% (July), and 59 and 7% (September).

Persistence of ERM populations.—There was considerable among-tree variation in the date after which no ERM were observed on the leaves; the range was from 23 August to 8 October. Although the difference was not statistically significant, there was a trend for populations on G-16 trees to persist longer into the fall (log-likelihood ratio test, $P = .12$). By 14 September, 81% of the populations on the G-16 trees were still present as compared with 68% of the G-1 populations. Two weeks later the percentage of persisting populations was 44% for G-16 vs. 21% for G-1 populations.

Temporal variance of ERM.—An estimate of the variability of ERM abundances over the season was obtained for each of the 51 target trees using a measure of temporal variance based on the standard deviation of log density with the spatial component removed (A. Stewart-Oaten et al., unpublished manuscript). There was some indication that group size might have affected the variability of the individual tree populations (ANOVA, $P = .10$), where G-16 trees were most variable. However, there was a significant and positive correlation between temporal variation and average abundance ($P < .001$), and after removing this dependence, temporal variability of populations on individual trees was not affected by the number of trees in the group (partial correlation, $P = .996$).

Similarity of populations within groups.—Similarity of ERM populations within groups was assessed by using ANOVA to calculate within-block correlation coefficients (r) for two variables, cumulative mite-days and temporal variability. Calculations were for the two target trees in each of the eight blocks of the G-4 and G-16 treatments. Two questions were of interest: (1) Are trees within a block more similar to each other than to trees in different blocks and (2) Are trees within G-16 blocks more similar to each other than are trees within G-4 blocks?

There was no evidence that trees in the same group had mite densities that were more similar than trees in different groups (G-4: $r = -0.009$, G-16: $r = -0.211$). G-16 trees were also no more similar in magnitude of temporal variability within than among blocks ($r = 0.266$, $P > .10$). Only populations within G-4 blocks were significantly more similar in temporal variability

TABLE 1. Effect of group size on percent of the European red mite (ERM) population in the egg, motile juvenile, and adult female stages in August sample. Values (means across trees) that share a common underline are not significantly different at $P = .05$ (ANOVA using arcsine square root transformation).

Mite life stage	Percent of population ($\bar{X} \pm$ SE)		
	G-1	G-4	G-16
Eggs	<u>93.4 \pm 2.0</u>	<u>91.4 \pm 2.4</u>	<u>83.6 \pm 1.7</u>
Motile	<u>3.8 \pm 1.4</u>	<u>4.2 \pm 1.0</u>	<u>12.0 \pm 1.3</u>
Adult female	<u>0.2 \pm 0.2</u>	<u>0.2 \pm 0.2</u>	<u>1.4 \pm 0.4</u>

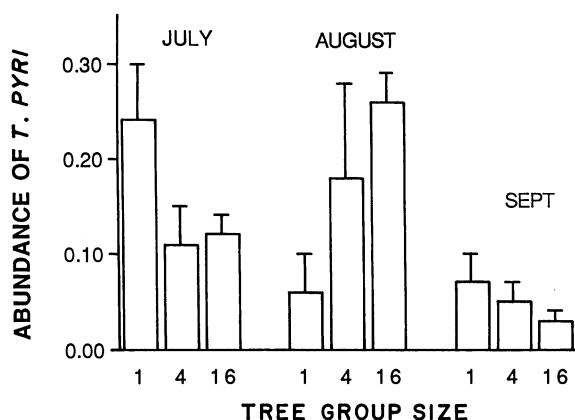


FIG. 3. Effect of tree group size on abundance of the predaceous mite *Typhlodromus pyri* (no./10 leaves) for three sampling dates. Error bars are standard errors. Significant differences ($P < .05$) were seen in July and August.

than populations in different blocks ($r = 0.628$, $P < .05$). This general absence of significant heterogeneity among blocks is surprising in light of the fact that the orchard was far from homogeneous in terms of soil, moisture, etc. To determine if the one significant effect with G-4 blocks might be due to this heterogeneity, I analyzed the front and back portions of the orchard (separated by a drainage ditch) independently. Within each half of the orchard, there was no evidence of within-block correlation (front: $r = -0.062$, back: $r = 0.061$). Finally, populations on trees in the larger groups (G-16) did not show greater similarity than populations in G-4 groups in either cumulative mite-days or temporal variability.

Predation

Abundance of T. pyri.—Number of trees in a group did affect the abundance of the predator, *T. pyri* (Fig. 3). There was a significant interaction between date and treatment for densities of *T. pyri* (repeated-measures ANOVA, $P < .001$). In July densities of predators were highest on the single trees ($P = .009$). By mid-season (August) densities were significantly higher on G-16 trees than on trees in the smaller groups ($P < .001$). By September predator densities did not differ among treatments.

Relative abundance of predator and prey.—I looked at the effect of group size and date (July, August, September) on two aspects of the relationship between predator and prey abundances: (1) the relative distributions of predator and prey (the slope of the regression of predator on prey abundance) and (2) whether there were, on average, more predators per prey on a tree (elevation of the regression of predator on prey numbers). Since *T. pyri* rarely consumes eggs or adult female ERM, I used number of juvenile ERM as the estimate of prey abundance.

The slope of the regression between predator and prey densities (fourth-root transformed) did not vary significantly with group size or date, suggesting that the relative spatial distributions of predator and prey did not vary with either factor. However, the elevation of the regressions did depend on both group size and date, indicating that there were, on average, more predators per prey on a tree in some treatments and on some dates (Table 2).

In July, there were significantly more predators per prey on the isolated trees (Table 2: column 1). In August the pattern reversed itself, with the highest predator-prey ratios on the trees in groups of 16. By September, the G-16 trees had the lowest predator-prey ratios once again.

The change over time in predator-prey ratio within group size treatments is perhaps the most interesting as it may reflect the numerical response of the predator. For trees in groups of 16, the predator-to-prey ratio increased from July to August and then decreased from August to September. Thus the highest predator-prey ratios were seen when prey densities were highest. In contrast, for G-1 trees, as prey densities increased from July to August, the number of predators per prey decreased. For G-4 trees, the predator-prey ratio neither increased nor decreased over the season.

Dispersal

Dispersal rates appeared to be very low in this orchard (average of <2 ERM caught per card), probably due to the fact that densities of ERM were relatively low.

Since ERM disperse primarily by wind, I first analyzed the number of mites arriving from each of the four cardinal directions, north, east, south, and west, regardless of whether the card was facing toward or away from a tree. There was an interaction between date and direction, with significantly more ERM arriving from the north and west in July, from the north, south, and west in August and from the south and west in September. This shift in direction corresponded to shifts in the direction of the prevailing winds in the area.

There was also a significant effect of group size, where cards associated with single trees had lower numbers

TABLE 2. Effect of group size and date on the relationship between predator and prey abundances. Values are elevations of regressions of predator density on juvenile prey density. Values sharing a common underline are not significantly different at $P = .05$. Within columns, values with the same lowercase letter are not significantly different.

Tree group size	No. predators per prey ($\bar{X} \pm \text{SE}$)		
	Jul	Aug	Sep
G-1	<u>.614 ± .038a</u>	<u>.159 ± .034a</u>	<u>.090 ± .167a</u>
G-4	<u>.201 ± .117b</u>	<u>.169 ± .017a</u>	<u>.133 ± .086a</u>
G-16	<u>.233 ± .034b</u>	<u>.300 ± .033b</u>	<u>.046 ± .009b</u>

than trees in groups ($P = .016$). When analyzed separately by direction, there were significantly more ERM from the north and east on cards in G-4 and G-16 trees than for single trees. There were no differences in number of ERM arriving from the south or west.

I then calculated an immigration index, averaging within a block the number of ERM caught on the side of the cards facing away from the trees. G-4 and G-16 trees had significantly higher immigration from the north than did single trees (Fig. 4; $P = .020$).

No *T. pyri* were caught on any card. To get an estimate of predator dispersal at these densities obviously required a more intensive sampling than the ≈ 240 cards per date used here.

DISCUSSION

It is well known that spatial heterogeneity of various sorts can influence the stability of populations. Much theory and empirical work (e.g., Bailey et al. 1962, Hassell and May 1973, 1974, May 1978, Chesson and Murdoch 1986, Kareiva and Odell 1987) has dealt with heterogeneity or patchiness on a relatively small spatial scale. At small scales movement of individuals among patches is expected to be frequent relative to generation time, and to be of major importance in influencing the dynamics of the population. As spatial scale becomes larger within-population processes are expected to become relatively more important, and predator and prey movements among patches are less frequent and less easily linked to behavior such as foraging. At large scales, then, the stability of the predator-prey interaction depends on dispersal and on the dynamics within the subpopulation.

In biological control, stability has long been considered desirable due to its presumed relationship with temporal variability, to the expectation that more stable populations are less likely to reach economically damaging levels. From a control point of view, then, measures of temporal variability and density (or the amount of time spent at high densities) are the variables of interest. In this study I have shown that altering the number of closely interacting subpopulations of mites in an apple orchard can affect the density of the pest population over a season. The observed pattern is, in part, opposite to that expected by theory. Trees in the largest groups had the most abundant (and thus the most variable populations) of the pest. This contrasts not only with theoretical expectations, but with the laboratory results of Pimentel et al. (1963) who found both lower average densities and lower variability in the systems with the greatest number of cells.

Dispersal patterns of ERM likely contributed to the observed differences in abundance. Wind direction was expected to influence dispersal, and I did see directional effects that shifted over the season. Within these directional patterns there were also significant effects of group size, where trees within groups appeared to have somewhat higher rates of immigration from at

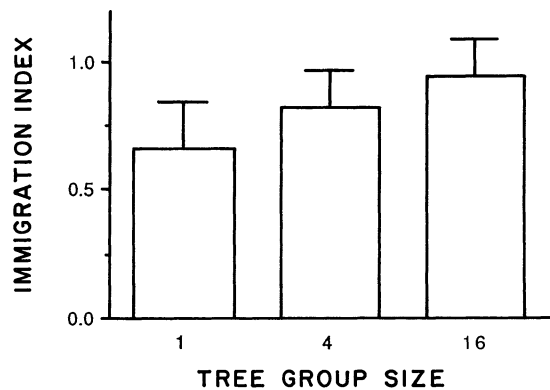


FIG. 4. Average effect of tree group size on index of immigration from the north. Error bars are standard errors.

least one direction. This suggests that one contributing factor to the pattern of abundances was a trapping effect of the group of trees. Dispersal of ERM is by wind, and therefore the mites have little control over where they end up. In a group of trees, however, it would be expected that some percentage of those blown from one tree would end up on another in the same group. The group as a whole, then, might retain a higher proportion of its mites than an isolated tree. Although I suggest a passive physical mechanism rather than a behavioral one, this explanation is similar to the one put forward by Kareiva (1985) where he argued that the lower perimeter/area ratios in larger patches will reduce emigration rate from the patch.

We have reason to believe that *T. pyri* has a major impact on ERM populations. Evidence from other orchards in eastern Canada and the northeastern United States suggests that it can control ERM populations when selective pesticides are used (Hardman et al. 1988, J. P. Nyrop, *personal communication*). And indeed, there is little doubt that ERM densities were "controlled" on trees in all treatments in this study, since even in the blocks with the highest ERM abundances, numbers never approached those seen in commercial orchards when the effectiveness of the predator is largely eliminated by pesticide use. This raises the question, then: Why, if *T. pyri* is acting as an effective control agent, was it unable to compensate for the rather slight increase in immigration by the pest?

Several other aspects of the observations in this study do not fit easily into the usual view of biological control. *T. pyri* does appear to respond numerically to its prey through the season as evidenced by the positive correlations with ERM densities. However, the numerical response typically associated with effective control agents, the highest predator-prey ratios coinciding temporally with the highest prey densities, occurred only on the G-16 trees. Furthermore, populations of ERM on G-16 trees had a lower proportion of edible juvenile stages in August, also suggesting heavier

predation. Despite this response, ERM populations reached their highest densities on G-16 trees.

I suggest that the observed patterns are consistent with the following scenario: *T. pyri* does not control the pest in the classical manner by imposing density-dependent mortality (either temporally or spatially). Rather, the pest goes through its seasonal cycle with population growth rates determined by food quality or abundance, and physical factors such as temperature. The predator takes some (usually high) portion of the prey production. At moderate ERM densities, mortality due to predation can depress the pest below the economic threshold. When the population growth rate of the prey is higher for some reason (immigration in this case), the predator does have a numerical response, but compensates too slowly, allowing the prey to reach higher maximum densities. The interaction is inherently unstable; the predator will eventually drive the prey extinct. This seemed to occur at the study site, where 75% of the trees had no ERM by 3 July of the following summer. The effect of dispersal is simply to delay this outcome.

This suggested scenario is, of course, only a hypothesis, one which requires further testing. At this point, however, it fits well with the observed results and with what is known about the dynamics of phytophagous mite populations. Unfortunately I was unable to obtain any data on dispersal rates for the predator and thus cannot evaluate the hypothesis that differences in predator immigration/emigration rates played a role in the outcome.

The observations differ from a priori expectations in that (1) low variability within a season is not associated with increased persistence, and (2) that in this case, at least, persistence may not be a desirable goal. The lack of concordance or equivalence among the concepts of mathematical stability (return of population to equilibrium), persistence, and temporal variability has been already noted many times (e.g., Reeve 1988, Murdoch and Walde 1989), and has been discussed specifically with respect to the theory of biological control (Murdoch 1989). The results of this study indicate that this lack of concordance is relevant to real systems, where low temporal variability is desirable and associated with the best level of control, but is negatively correlated with both persistence and stability and positively correlated with the probability of extinction.

The dynamics of the ERM-*T. pyri* system described in this study is somewhat suggestive of metapopulation dynamics, where individual populations may be unstable, but the ensemble is stabilized through dispersal among populations. There is an indication of instability in the ERM-*T. pyri* interaction, where it appears that the predator may drive the pest extinct on the spatial scale of a tree. Stability of the ensemble requires, however, enough dispersal that recolonization occurs, but not so much that the populations become syn-

chronized. In this study, populations on trees within groups were not any more similar than populations in different groups, suggesting that dispersal did not synchronize populations within groups.

Does this type of dynamics actually result in good control or will the pest resurge in subsequent years? Studies that have looked at the effects of broad-spectrum insecticide usage (e.g., Pickett and Patterson 1953, Lord 1956, Sanford and Herbert 1967) as well as current anecdotal information from growers who raise apples in this region without pesticides indicates that ERM typically does not resurge. It does not seem to become extinct across an entire orchard, but rarely, if ever, reaches economically important levels. Extinction of the pest, local or otherwise, is, of course, probably not the desirable goal of all biological control programs. For example, the fact *T. pyri* is a generalist rather than a specialist and thus may be able to persist at relatively high densities despite the low abundance of ERM probably contributed to the success of this particular system with these dynamics. However, it would seem that there are likely to be a variety of dynamical patterns that are compatible with successful biological control, and the first step toward understanding how or why a particular system works will have to be to determine which dynamical mechanisms are operating.

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