

# Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system

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## Summary

1. Functional and numerical responses are key components in the selection of predators for biological control. We examined the relevance of these responses for predicting the effectiveness of generalist predators, taking into account effects of alternative prey and multiple predators. Our system involved two acarine predators of two prey species on apple. Responses were measured on leaf discs in the laboratory, and predictions assessed on small potted apple trees. In particular, we tested three hypotheses.

2. Hypothesis I: the species with the higher predatory responses will be more effective in limiting prey populations. Neither predator had a consistently higher functional response, which depended on prey stage and species. *Amblyseius fallacis* had a (approximately two times) higher ovipositional response than *Typhlodromus pyri*. We therefore hypothesized that *A. fallacis* would be more effective in controlling prey. No evidence was found to support this hypothesis.

3. Hypothesis II: alternative prey reduce the functional response of predators to target prey. Alternative prey did or did not reduce the functional response to target prey, depending on the predator, stage and species of alternative prey. The only consistent trend for both predators was that the predation of *Panonychus ulmi* deutonymphs was reduced when *Tetranychus urticae* was present.

4. Hypothesis III: the predator species with the highest mean ovipositional response will out-compete the other predator species. The number of predators observed in the mixed predator treatments depended on the prey composition. Although *A. fallacis* had a higher ovipositional response, it was never more abundant. Intraguild predation probably played a role in determining predator abundance, although prey composition altered intraguild effects.

5. These results highlight the complex nature of predator and prey interactions. Because of these interactions, functional and numerical assays on single predator–single prey systems in simplified laboratory environments do not allow predictions of the growth of mixed populations in realistic habitats, or of the effectiveness of predators as biological control agents in the field.

*Key-words:* Acari, alternative prey, generalist predators, intraguild effects.

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## Introduction

Ecologists have focused extensively on functional and numerical responses as a means of assessing the impact of a natural enemy on a prey population. The

functional response relates to the change in predation rate with changing prey density. The numerical response is defined as the change in reproductive rate with changing prey density, although it can also include effects of immigration (Solomon 1949; Holling 1959). Three factors contribute to changes in the functional and numerical response of predators. First, predators may reduce their migration rate with increasing prey densities (Zemek & Nachman 1998).

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Secondly, Murdoch (1971) has suggested a developmental response, in which predators can grow faster at higher prey densities. Finally, predators may interfere with each other's foraging and reduce the functional response of each individual predator in a population (Abrams & Ginzburg 2000). The combined influence of these factors on a predator's response to prey density has been referred to as the total response (Price 1997).

The polyphagous nature of many natural enemies is an issue of critical importance for researchers in biological control (Simberloff & Stiling 1996). Predators released in biological control programmes are often generalists, consuming a wide variety of prey species. These generalist predators may significantly reduce populations of non-target organisms through direct predation (Civeyrel & Simberloff 1996) or competition (Elliott, Kieckhefer & Kauffman 1996). Consequently, predators released for biological control that attack non-target or alternative prey may become pests themselves and contribute little to the control of the target species (Louda *et al.* 1997).

Theoretical contributions to the effects of alternative prey on the population dynamics of a target prey have focused on the functional and numerical response (Chesson 1989; Foglar, Malausa & Wajnberg 1990; Eubanks & Denno 2000). The functional response has been utilized extensively as a tool to assess the potential of natural enemies to control pest species (Barlow & Goldson 1993; Lester *et al.* 1999). The primary effect of alternative prey on the functional response is a decrease in the consumption of the primary prey due to switching or satiation (Murdoch 1969; Murdoch & Oaten 1975).

A decrease in target prey consumption as a result of alternative prey may be considered a short-term negative impact on biological control. However, alternative prey can contribute positively to biological control by increasing a predator's numerical response. Settle *et al.* (1996) observed an increased abundance of alternative prey by adding organic material to a rice field. The alternative prey allowed a 'head-start' in abundance for generalist predators, which were then more abundant and effective in controlling pest species later in the growing season. While the density of polyphagous predators was increased, that of monophagous parasitoids was unaffected or slightly reduced by the presence of alternative prey (Settle *et al.* 1996). The inability of species to utilize alternative prey has been estimated to account for 17% of failures of natural enemy establishment in biological control programmes (Stiling 1993). Alternative prey may thus be a positive or negative influence on biological control.

Stiling (1993) also suggested that a further 20% of failed introductions were due to predation or parasitism of the introduced natural enemy by native fauna. The diet of many predator species broadly incorporates many different feeding guilds. The act of a predator

consuming other predators has been referred to as intraguild predation (Rosenheim *et al.* 1995). The extent of intraguild predation has led researchers to consider some generalist predators as poor biological control agents (Riechert & Lockley 1984). Hypotheses for the failure of predators to exert biological control often involve intraguild predation (González-Hernández, Johnson & Reimer 1999; Snyder & Wise 1999). These studies are examples of instances where intraguild predation can increase the abundance of the extraguild prey. However, intraguild predation may also have negligible effects on biological control (Parrella, McCaffrey & Horsburgh 1980) or may result in increased biological control of a pest population (Geden, Stinner & Axtell 1988).

In summary, the ability of a predator to control prey is dependent on the predator's functional and numerical response. However, these responses are influenced by a variety of factors, including the behavioural patterns in response to its own densities, the developmental response, preference and utilization of alternative prey, and a predator's interaction with other predators. Yet, scientists involved with biological control programmes commonly assess the potential of a predator using functional response studies with an individual predator feeding on a single patch of a prey species (Harms & Johansson 2000; Lester, Thistlewood & Harmsen 2000; Montserrat, Albajes & Castane 2000; Pichlova & Vijverberg 2001). There is some indication that such laboratory analyses of functional responses may be of limited use in assessing the effects of predators in field conditions (O'Neil 1997). Here, our primary question was how useful is a laboratory analysis of functional and numerical responses in determining the potential of a natural enemy for effective biological control? We tested three hypotheses: I, the species with the higher predatory responses will be more effective in limiting prey populations; II, alternative prey reduce the functional response of predators on target prey; and III, the predator species that has the highest mean ovipositional response will out-compete the other predator species.

#### STUDY SYSTEM

Two species of phytophagous mites, *Panonychus ulmi* (Koch) and *Tetranychus urticae* (Koch) (Acari: Tetranychidae), are commonly observed in stonefruit and pipfruit orchards of Ontario, Canada (Putman & Herne 1966; Lester, Thistlewood & Harmsen 1998). Of the two species, *P. ulmi* is generally more abundant and more commonly pestiferous. Predatory mites of the family Phytoseiidae have been considered for biological control of these mites. Two such species are *Amblyseius fallacis* (Garman) and *Typhlodromus pyri* (Scheuten) (Acari: Phytoseiidae). *Amblyseius fallacis* has been suggested to prefer *Te. urticae*, and *Ty. pyri* to prefer *P. ulmi* (Putman & Herne 1966; Herbert 1959; Dicke & De Jong 1988).

## Methods

### MITE COLONIES

The *A. fallacis* colony was started in 1993 from mites collected in Jordan, Ontario, Canada (Thistlewood, Pree & Crawford 1995). The *Ty. pyri* colony originated from New Zealand and had recently been used successfully for biological control in Nova Scotia, Canada (Hardman *et al.* 1997). Both predator colonies were reared in units consisting of a water-soaked sponge within a pie-pan surrounded by a water moat, at  $24 \pm 1$  °C, 60% relative humidity (RH) and 16 : 8 (light : dark; L:D) h. Three times weekly, leaves of the kidney bean *Phaseolus vulgaris* L. infested with *Te. urticae* were added to each rearing unit. Changing the host-plant may influence the functional and numerical response of phytoseiid mites (Lester, Thistlewood & Harmsen 2000). In an attempt to circumvent these effects, eggs of predators were transferred to and raised on individual excised apple *Malus domestica* Borkhauser cv. Empire leaves on wet cotton wool 2 weeks prior to experimentation. These predators were grown for 2 weeks at the above conditions on a mixed prey population of both *Te. urticae* and *P. ulmi* immediately prior to being used. The *Te. urticae* colony was grown on kidney bean plants at  $24 \pm 1$  °C, 60% RH and 16 : 8 (L:D) h. The *P. ulmi* was reared on peach tree *Prunus persica* (L.) Batsch seedlings at  $24 \pm 2$  °C, 60% RH and in continuous light.

### PREDATOR RESPONSE ANALYSIS

We compared the functional and numerical response of adult female *A. fallacis* and *Ty. pyri* feeding on *P. ulmi* and *Te. urticae* eggs and deutonymphs. These prey life stages were chosen as they represented very different life stages of the prey species. The prey densities selected were 2, 6, 14, 26 or 40 per leaf disc for eggs, and 1, 5, 9, 15 or 25 per leaf disc for deutonymphs. These densities were examined for each prey species alone, or in a mixture of 1, 5, 9, 15 or 25 of both prey species on the same leaf disc. All experiments were undertaken on 1.2-cm diameter (total surface area =  $1.13 \text{ cm}^2$ ) apple cv. 'Empire' leaf discs. These leaf discs were placed on wet cotton wool, which restricted mite movement to the disc. All prey were transferred from the leaves of their host-plant onto the apple leaf discs with a fine paint brush. The consumption by predators of each prey was recorded once daily, after which the prey density was readjusted to the target density. Predator eggs were also counted daily and removed. For each prey density and predator treatment, four replicate tests were undertaken. The predators were preconditioned for 2 days, then data were collected for 3 consecutive days.

Type II functional responses were modelled using the equation of Rogers (1972):

$$N_a = N\{1 - \exp[-aT/(1 + aT_h N)]\} \quad \text{eqn 1}$$

where  $N_a$  is the number of prey attacked,  $N$  is the number of prey available, and  $T$  is time (1 day). The parameters  $a$  (the rate of successful attack) and  $T_h$  (the time required to handle a prey item) were calculated using least-squares non-linear regression, using the quasi-Newton estimate method (Statsoft 1995).

To examine the relationship between oviposition and prey density, we used the equation of Nwilene & Nachman (1996):

$$E = e_1 N^b - e_0 (E \geq 0) \quad \text{eqn 2}$$

where  $e_1$  is a constant expressing the predator's efficiency of converting prey into predator eggs, and  $e_0$  is the metabolic cost per unit time measured in terms of reduced fecundity (predator eggs per time unit). The parameters  $e_1$ ,  $b$  and  $e_0$  were estimated using least-squares non-linear estimation as described above.

Two-way repeated-measures ANOVAS were used to examine the effects of alternative prey on the functional response of *P. ulmi* and *Te. urticae*. The dependent variable was the number of the target species killed each day. The independent variables in this analysis were 'prey treatment' and 'prey density'. The prey treatment factor was the presence or absence of alternative prey (*Te. urticae* in the analysis of *P. ulmi* or vice versa). Separate ANOVAS were performed for each prey and prey stage combination. A similar analysis was performed for the ovipositional data, except that the dependent variable was the number of eggs produced each day. Data were not log transformed, as we wanted to examine additive effects of alternative prey rather than multiplicative effects. For both the functional and oviposition response analyses, data from 3 consecutive days were used in the repeated-measures analysis, after 2 days of preconditioning to the leaf and prey densities.

### POTTED TREE EXPERIMENT

Experiments comparing the predators feeding on *Te. urticae* and *P. ulmi* were undertaken on small individually potted apple cv. 'Empire' trees. Each tree had approximately 20 leaves. Plant and mites were maintained in a room with controlled temperature ( $24 \pm 1.5$  °C) and humidity ( $70 \pm 5\%$ ) at an illuminance of  $130 \mu \text{ Einsteins m}^2 \text{ s}^{-1}$  on a 16 : 8 (L:D) h cycle. Plants were watered daily, and fertilized prior to the experiment.

In an attempt to limit mite movement between plants a plastic collar filled with a water barrier was fitted to each plant. This collar was made from a 1-ml pipette tip that was sliced longitudinally to fit around the base of the tree stem. Once on the plant, the collar was sealed with Vaseline®-saturated cotton wool and filled with water daily. To limit air movement and mite migration between plants further, large polyethylene 'Vapor Barrier' plastic [150  $\mu\text{m}$  thickness; W. Ralston (Canada) Inc., Brampton, Canada] sheets were erected within

the room. These sheets were painted with Tanglefoot® (The Tanglefoot Company, Grand Rapids, MI) to catch any mites that may have been migrating aerially within the room.

Plants were assigned randomly to three prey treatments: *P. ulmi* alone, *Te. urticae* alone, or *P. ulmi* and *Te. urticae* together. To add *P. ulmi* and *Te. urticae* to the seedlings, leaves were excised from the laboratory colonies and tied to the seedlings. For each of the three prey treatments there were four predator treatments: no predators (control), *A. fallacis* alone, *Ty. pyri* alone, and *A. fallacis* and *Ty. pyri* together. In all treatments 10 predators were added per seedling (*c.* 0.5 leaf<sup>-1</sup>). In the *A. fallacis* and *Ty. pyri* treatment, five of each species were added to each tree. Five replicate seedlings were used in each treatment.

Trees were sampled for prey prior to the predators being added. From each seedling one leaf was excised and examined under a binocular microscope at ×20 magnification. After predator inoculation, seedlings were sampled similarly on a weekly basis for 5 weeks. Predators sampled were always returned to their respective plants, otherwise such sampling may have significantly reduced the predator population. As *A. fallacis* and *Ty. pyri* are indistinguishable under a binocular microscope, the predator estimate on the mixed predator treatment was of total phytoseiid abundance rather than individual predator abundance. Eggs and mobile stages of each species were combined to give one density estimate per taxon.

On the last sample taken from the seedlings, 5 weeks after the initiation of the study, five leaves were sampled and mite densities estimated from these. For the predator treatments with both *A. fallacis* and *Ty. pyri*, all leaves were removed from the trees and examined for phytoseiids. These predators were mounted on glass slides in Hoyer's medium (Beek 1955), placed for 1 week on a slide-warmer at approximately 45 °C, and identified. Similarly, a sample of 10

phytoseiids was sampled from each of the other predator treatments to ensure that no predator species had moved between treatments.

Statistical analysis was undertaken separately on the sample of mites prior to and after predator inoculation. For the sample prior to predator inoculation, two-way ANOVA was used to examine for differences in *P. ulmi* or *Te. urticae* densities between treatments. The factors for this ANOVA were predator treatment (none, *A. fallacis*, *Ty. pyri*, and mixed *A. fallacis* and *Ty. pyri*) and prey treatment (either *P. ulmi* or *Te. urticae* singly, or together). The same factors were used in the analysis of mite densities at the end of the experiment. However, in this analysis a two-way repeated-measures ANOVA was used, with each of the 5-week data used as the repeated-measures factor.

## Results

### HYPOTHESIS 1: THE SPECIES WITH THE HIGHER PREDATORY RESPONSES WILL BE MORE EFFECTIVE IN LIMITING PREY POPULATIONS

The predator with the highest functional response differed between the prey species treatments. For the predators consuming eggs, *A. fallacis* had a significantly higher functional response than *Ty. pyri* when feeding on *P. ulmi* eggs (Table 1 and Fig. 1). When consuming *Te. urticae* eggs, *Ty. pyri* had a higher functional response than *A. fallacis*. However, differences in the consumption of individual *Te. urticae* eggs were noted between predator species. Almost no trace of the egg remained after consumption by *A. fallacis*. In contrast, *Te. urticae* eggs eaten by *Ty. pyri* were not entirely consumed. For some *Te. urticae* eggs, at least half the contents remained after the *Ty. pyri* had moved on to other eggs. A sample of these partially consumed eggs retained for 2 weeks after *Ty. pyri* attack did not hatch

**Table 1.** Results from repeated-measures ANCOVA comparing the functional and ovipositional responses of *A. fallacis* and *Ty. pyri*. Each row represents the results from an individual ANCOVA, where the dependant variable was the number of prey consumed per day. The independent variable was 'predator species', the repeated-measures effect was 'time' and the covariate was 'prey density'. \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001

| Prey species           | Prey stage  | ANOVA effects ( <i>F</i> -values) |       |                     | Tukey ( <i>P</i> < 0.05) tests<br>on number of prey consumed |
|------------------------|-------------|-----------------------------------|-------|---------------------|--|
|                        |             | Predator                          | Time  | <i>P</i> × <i>T</i> |  |
| Functional response    |             |                                   |       |                     |  |
| <i>P. ulmi</i>         | Eggs        | 34.95***                          | 4.68* | 6.24**              | A.f. (6.7) > T.p. (3.6)                                      |
|                        | Deutonymphs | 6.47*                             | 1.51  | 1.56                | A.f. (3.7) = T.p. (4.8)                                      |
| <i>Te. urticae</i>     | Eggs        | 9.77**                            | 2.02  | 1.14                | A.f. (4.4) < T.p. (8.7)                                      |
|                        | Deutonymphs | 0.13                              | 1.11  | 1.5                 | A.f. (4.2) = T.p. (4.0)                                      |
| Ovipositional response |             |                                   |       |                     |  |
| <i>P. ulmi</i>         | Eggs        | 10.84**                           | 0.25  | 0.32                | A.f. (0.9) > T.p. (0.4)                                      |
|                        | Deutonymphs | 1.92                              | 2.39  | 2.15                | A.f. (1.1) = T.p. (0.9)                                      |
| <i>Te. urticae</i>     | Eggs        | 9.82*                             | 0.66  | 0.15                | A.f. (0.4) = T.p. (0.1)                                      |
|                        | Deutonymphs | 20.75***                          | 0.81  | 1.13                | A.f. (1.4) > T.p. (0.7)                                      |

T.p., *Ty. pyri*; A.f., *A. fallacis*.

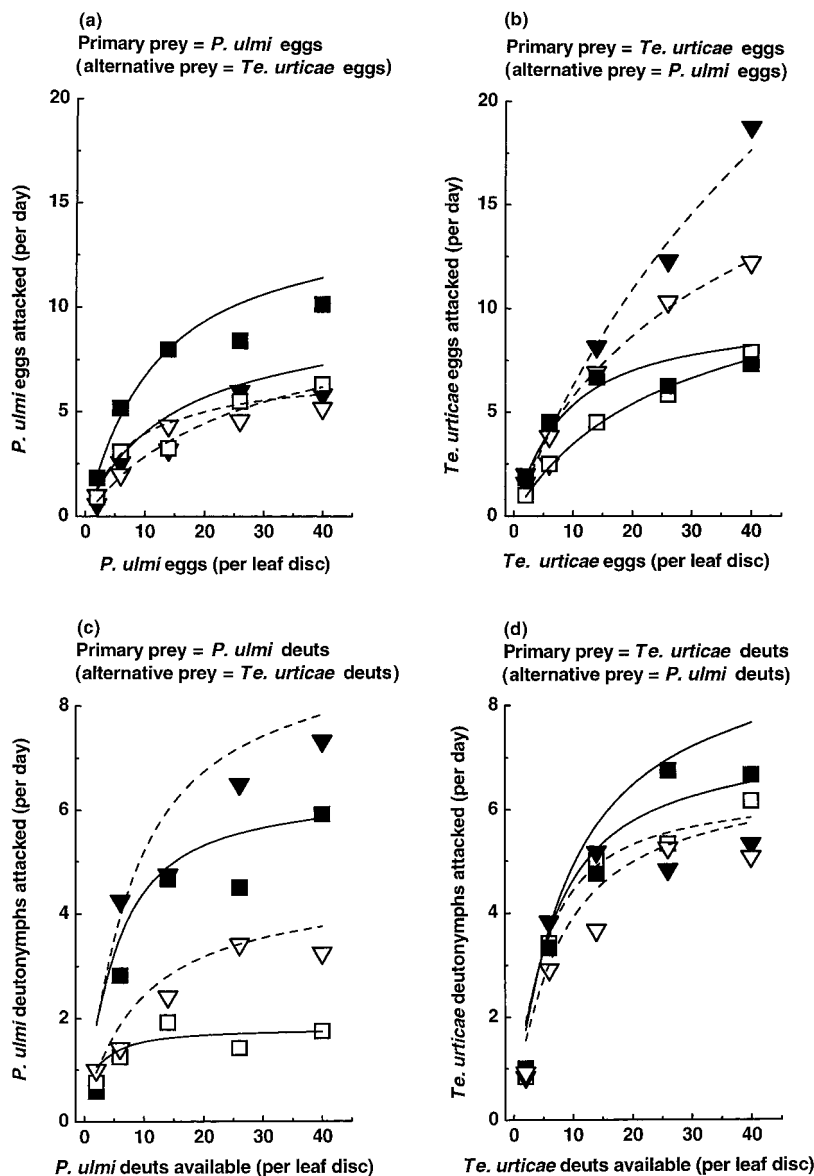


Fig. 1. The functional response of the predators on target prey alone, or prey with an alternative prey present. Black triangles, the response of *Ty. pyri* on primary prey alone; white triangles, the response of *Ty. pyri* on primary prey in the presence of alternative prey; black squares, the response of *A. fallacis* on primary prey alone; white squares, the response of *A. fallacis* on primary prey in the presence of alternative prey. Depts, deutonymphs. Values are means,  $n = 4$ .

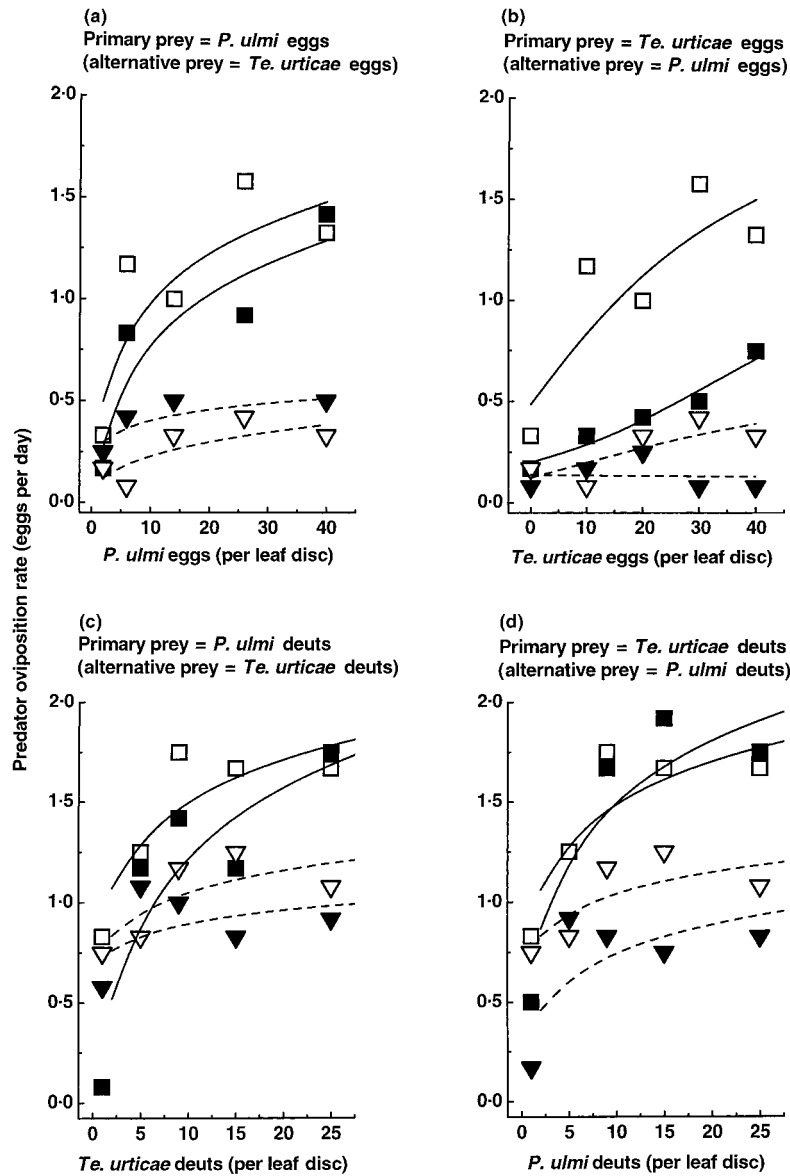
into larvae. These eggs were thus considered ‘consumed’ in the functional response analysis.

When the predators were feeding on deutonymphs, *Ty. pyri* was observed to eat a mean of 1.3 times as many *P. ulmi* as *A. fallacis*. However, both species consumed a similar number of *Te. urticae* deutonymphs (Table 1 and Fig. 2).

For all prey stages and prey species, *A. fallacis* consistently had a higher ovipositional response than *Ty. pyri* (Table 1 and Figs 1 and 2). For the ovipositional response with eggs as prey, *Ty. pyri* had a relatively small ovipositional response to *Te. urticae* eggs alone (Fig. 1). *Tetranychus urticae* eggs thus appeared to contribute little nutritional value to *Ty. pyri*. For three of the four prey species treatments, *A. fallacis* had a significantly higher ovipositional response by a factor of at least two. It would thus seem logical to predict that

*A. fallacis* would be more effective in limiting prey populations on the small potted trees.

Prior to the inoculation of predators on the potted trees, no significant differences ( $P > 0.05$ ) were observed in the densities of either *P. ulmi* or *Te. urticae* between any predator or prey treatment. Differences between treatments began to appear soon after predator inoculation. In the *A. fallacis* treatments of the potted tree experiment, the peak density of *P. ulmi* was  $124 \pm 47$  in the single prey treatment, while in the mixed populations it was  $148 \pm 48$ . When *A. fallacis* was consuming *Te. urticae* as the target prey, the peak *Te. urticae* density was  $148 \pm 59$  in the single prey treatment, while in the mixed prey treatment it was  $79 \pm 28$  (Fig. 3). In the *Ty. pyri* treatments, the highest density of *P. ulmi* in the single prey treatment was observed at  $226 \pm 86$ , compared with  $68 \pm 14$  in the mixed prey



**Fig. 2.** The ovipositional response of the predators on target prey alone, or prey with an alternative prey present. Black triangles, the response of *Ty. pyri* on primary prey alone; white triangles, the response of *Ty. pyri* on primary prey in the presence of alternative prey; black squares, the response of *A. fallacis* on primary prey alone; white squares, the response of *A. fallacis* on primary prey in the presence of alternative prey. Deuts, deutonymphs. Values are means,  $n = 4$ .

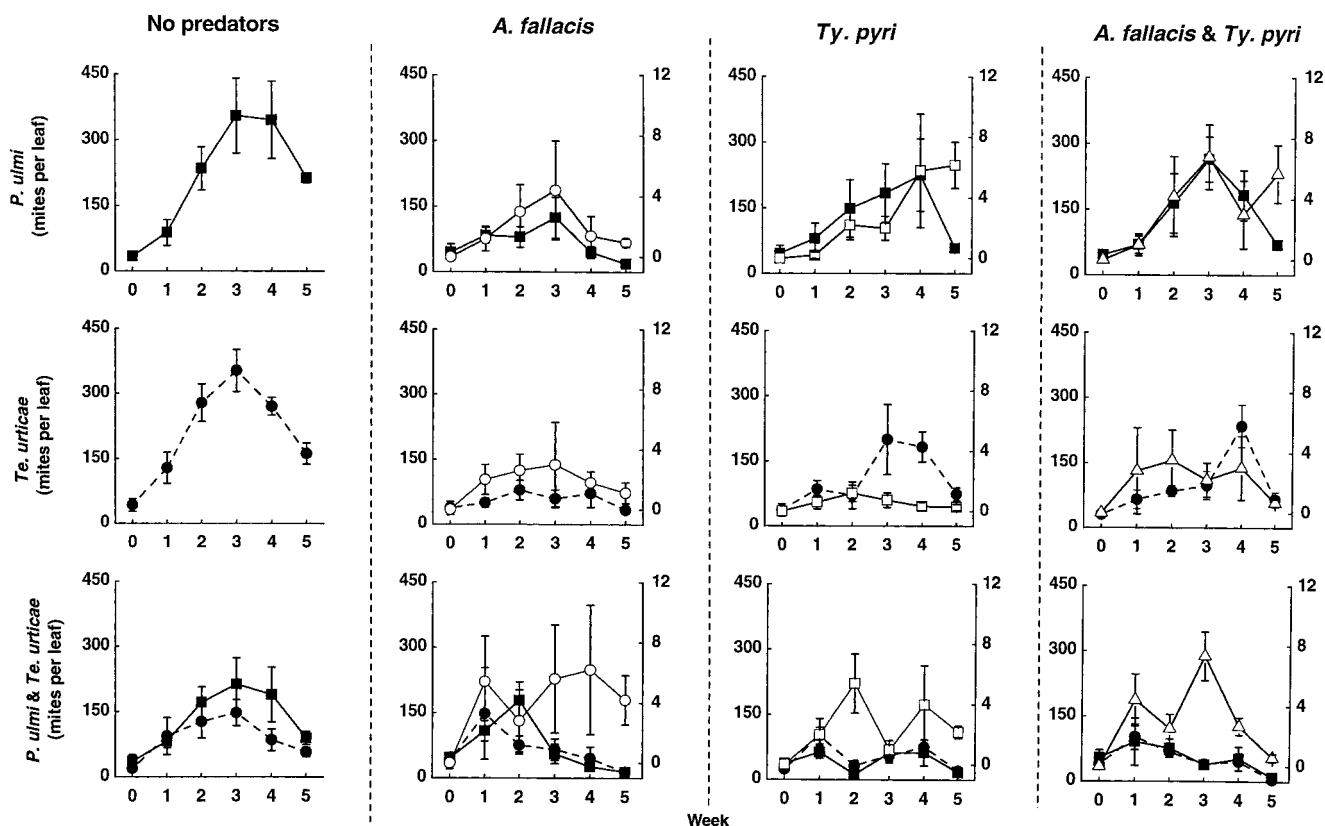
treatment. For *Ty. pyri* and *Te. urticae* treatments, the peak *Te. urticae* density was  $201 \pm 85$  in the single prey treatment, while in mixed populations it was  $101 \pm 19$  (Fig. 3).

The differences between treatments of the potted tree experiment were analysed by two-way repeated-measures ANOVA. Similar results were observed for analyses on both *P. ulmi* and *Te. urticae*. A significant effect of predator species in this ANOVA did not show differences between predator species, rather it indicated that the number of phytophagous mites was significantly higher in the control treatment that had no predators (Table 2). Thus, our data did not support the hypothesis that the species with the higher predatory responses will be more effective in limiting prey populations. Significant predator  $\times$  day, and prey  $\times$  day interactions were observed. An examination of the

means indicated that these were initially due to increasing densities of these populations over time, followed by a decrease in some of these populations at the end of the study period. A significant predator  $\times$  prey interaction term in the ANOVA examining *P. ulmi* is discussed below.

#### HYPOTHESIS II: ALTERNATIVE PREY REDUCE THE FUNCTIONAL RESPONSE OF PREDATORS ON TARGET PREY

We observed situations in which the functional response of both predator species was or was not significantly reduced ( $P < 0.17$ ) by the presence of alternative prey. The effects of alternative prey on predation were complex and clearly specific to each prey stage, prey species and predator.



**Fig. 3.** Mean densities of prey (left x-axis) and predator (right x-axis) species on the small potted apple trees. The graphs are divided into four columns with one for each predator treatment: no predators, *A. fallacis*, *Ty. pyri*, and both predators. The three graphs within each column are for the three prey treatments: *P. ulmi*, *Te. urticae*, and both prey. Error bars are standard error,  $n = 5$ .

**Table 2.** Two-factor repeated-measures ANOVA on *P. ulmi* or *Te. urticae* densities from the potted tree experiment. Prey (for the *P. ulmi* model): either *P. ulmi* alone or together with the same density of *Te. urticae*. Prey (for the *Te. urticae* model): either *Te. urticae* alone or together with the same density of *P. ulmi*. Predator treatments: no predator, *A. fallacis*, *Ty. pyri*, or both predators together. Significance of *F*-statistics: \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , MS = mean square

| Source of variation                         | d.f. (effect) | MS (effect) | <i>F</i> -statistic | Tukey test ( $P < 0.05$ ) (Tukey test means in parentheses)              |
|---|---------------|-------------|---------------------|--|
| <i>P. ulmi</i> ( $\pm$ <i>Te. urticae</i> ) |               |             |                     |  |
| Prey  | 1             | 5.09        | 28.01***            | Alone (152) > mixed (9 = 80)   |
| Predator                                    | 3             | 2.89        | 15.89***            | None (197) > <i>Ty. pyri</i> (91) = <i>A. fallacis</i> (73) = both (102) |
| Prey $\times$ predator                      | 3             | 0.74        | 4.07**              |  |
| Time  | 4             | 1.4         | 19.97***            |  |
| Prey $\times$ time                          | 4             | 0.47        | 6.69***             |  |
| Predator $\times$ time                      | 12            | 0.48        | 6.85***             |  |
| Prey $\times$ predator $\times$ time        | 12            | 0.13        | 1.82                |  |
| <i>Te. urticae</i> ( $\pm$ <i>P. ulmi</i> ) |               |             |                     |  |
| Prey  | 1             | 24.96       | 19.14***            | Alone (127) > mixed (65)   |
| Predator                                    | 3             | 16.16       | 12.39***            | None (172) > <i>Ty. pyri</i> (81) = <i>A. fallacis</i> (56) = both (75)  |
| Prey $\times$ predator                      | 3             | 1.30        | 0.59                |  |
| Time  | 4             | 5.48        | 12.49***            |  |
| Prey $\times$ time                          | 4             | 3.48        | 7.93***             |  |
| Predator $\times$ time                      | 12            | 1.41        | 3.21***             |  |
| Prey $\times$ predator $\times$ time        | 12            | 0.86        | 1.97                |  |

When *P. ulmi* eggs were the target prey and *Te. urticae* eggs were present as alternative prey, the functional response of *A. fallacis* was significantly reduced to approximately half that observed when *P. ulmi* eggs were presented alone (Table 3 and Fig. 1). However, *Ty. pyri*'s consumption rate of *P. ulmi* was not significantly

reduced by the presence of *Te. urticae* eggs. This was in contrast to results obtained when *Te. urticae* was considered the primary prey species. For both *A. fallacis* and *Ty. pyri*, no significant reduction in the functional response to *Te. urticae* eggs was observed when *P. ulmi* eggs were present as alternative prey.

**Table 3.** Effects of alternative prey on the functional response, from the repeated-measures ANOVA. Each row represents the results from an individual ANOVA, where the dependent variable was the number of prey consumed per day. The independent variables were 'prey density' and 'alternative prey'. Alternative prey treatments were the prey species presented with or without the same stage of the other prey species. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

| Predator           | Prey               | Stage       | ANOVA effects ( $F$ -values) |              |   |                   |
|--------------------|--------------------|-------------|------------------------------|--------------|---|-------------------|
|                    |                    |             | Alternative prey             | Prey density | Alternative prey $\times$ density interaction | Repeated measures |
| <i>Ty. pyri</i>    | <i>P. ulmi</i>     | Eggs        | 0.29                         | 20.11***     | 1.28  | 7.33              |
|                    |                    | Deutonymphs | 61.41***                     | 24.29***     | 4.66*   | 4.15*             |
|                    | <i>Te. urticae</i> | Eggs        | 0.86                         | 8.53***      | 0.62  | 0.59              |
|                    |                    | Deutonymphs | 1.71                         | 23.14***     | 1.09  | 1.21              |
| <i>A. fallacis</i> | <i>P. ulmi</i>     | Eggs        | 87.00***                     | 58.61***     | 4.60**  | 2.64              |
|                    |                    | Deutonymphs | 131.25***                    | 31.06***     | 13.71***                                      | 0.05              |
|                    | <i>Te. urticae</i> | Eggs        | 6.39*                        | 31.84***     | 1.79  | 4.16*             |
|                    |                    | Deutonymphs | 2.35                         | 77.55***     | 1.68  | 0.13              |

**Table 4.** Effects of alternative prey on the oviposition of the predators, from the repeated-measures ANOVA. Each row represents the results from an individual ANOVA, where the dependent variable was the number of prey consumed per day. The independent variables were 'prey density' and 'alternative prey'. Alternative prey treatments were the prey species presented with or without the same stage of the other prey species. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

| Predator           | Prey               | Stage       | ANOVA effects ( $F$ -values) |              |   |                   |
|--------------------|--------------------|-------------|------------------------------|--------------|---|-------------------|
|                    |                    |             | Alternative prey             | Prey density | Alternative prey $\times$ density interaction | Repeated measures |
| <i>Ty. pyri</i>    | <i>P. ulmi</i>     | Eggs        | 1.75                         | 0.67         | 0.23  | 0.61              |
|                    |                    | Deutonymphs | 0.78                         | 0.96         | 0.51  | 0.54              |
|                    | <i>Te. urticae</i> | Eggs        | 2.59                         | 0.64         | 0.77  | 1.19              |
|                    |                    | Deutonymphs | 5.79*                        | 2.43         | 0.78  | 1.41              |
| <i>A. fallacis</i> | <i>P. ulmi</i>     | Eggs        | 2.47                         | 8.03***      | 0.93  | 0.06              |
|                    |                    | Deutonymphs | 8.80**                       | 17.11***     | 1.91  | 1.26              |
|                    | <i>Te. urticae</i> | Eggs        | 24.14***                     | 4.82**       | 1.32  | 0.61              |
|                    |                    | Deutonymphs | 0.02                         | 12.23***     | 0.63  | 0.73              |

Despite the result that *Te. urticae* appeared to contribute little to the ovipositional response of *Ty. pyri*, this predator continued to attack *Te. urticae* eggs even in the presence of *P. ulmi* eggs. The ovipositional response to prey eggs by *Ty. pyri* reached a maximum of only  $0.50 \pm 0.22$  eggs day<sup>-1</sup> in the *P. ulmi* alone treatment. The presence of alternative prey eggs did not significantly increase the ovipositional response of *Ty. pyri* (Table 4). In comparison, *A. fallacis* had a much higher ovipositional response that was affected by alternative prey. The highest oviposition rate of *A. fallacis* was  $1.58 \pm 0.08$  in the mixed egg treatment, which was over three times that of *Ty. pyri*. Similarly to *Ty. pyri*, the lowest ovipositional rate of *A. fallacis* was observed on a diet of *Te. urticae* eggs. The ovipositional response of *A. fallacis* was increased by an average factor of 2.7 when *P. ulmi* eggs were provided as alternative prey with *Te. urticae* eggs (Fig. 1). The low ovipositional response of both predators to *Te. urticae* eggs indicated that these may be a poor food source.

When the predators were placed with deutonymphs as prey, both exhibited a similar functional response and a similar change in consumption as a result of

alternative prey. With *P. ulmi* deutonymphs as the target prey, the presence of *Te. urticae* significantly reduced *P. ulmi* consumption by approximately half for both predators (Table 3 and Fig. 2). Alternatively, for both predators the consumption of *Te. urticae* was similar whether they were alone or with *P. ulmi* as alternative prey (Fig. 2).

Distinct differences in oviposition behaviour were noted as a result of alternative prey. For *Ty. pyri*, the presence of *P. ulmi* as alternative prey significantly increased the oviposition rate compared with when *Te. urticae* was presented alone. The presence of *P. ulmi* as alternative prey with *Te. urticae* deutonymphs had no significant effect with *A. fallacis* as the predator (Table 4 and Fig. 2). However, for *A. fallacis* the presence of *Te. urticae* as alternative prey with *P. ulmi* significantly increased the oviposition rate (Table 4 and Fig. 2).

Thus, we can accept the hypothesis that alternative prey can reduce the functional response, or increase the numerical response, of predators. However, we cannot generalize on the effects of alternative prey for either predator. Both predators showed different effects of

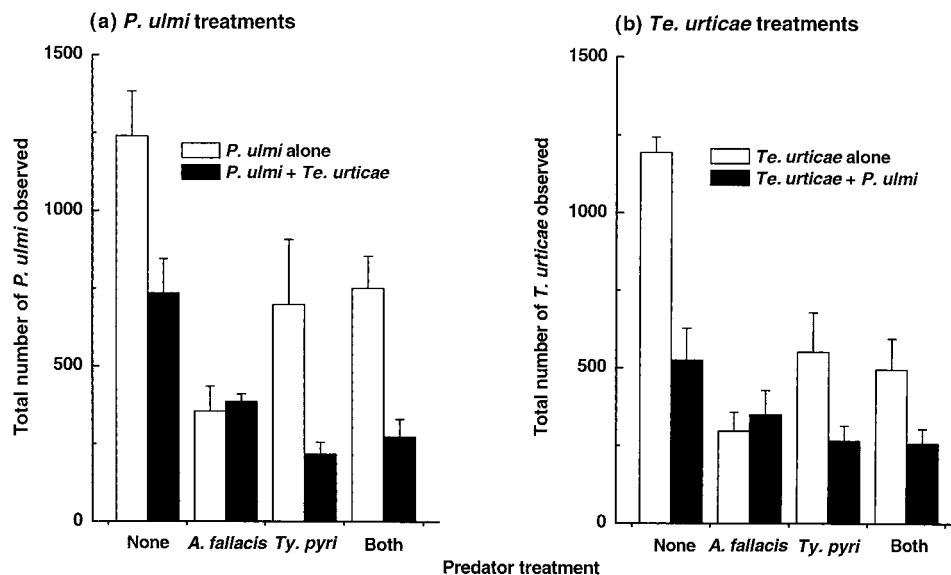


Fig. 4. The total number of *P. ulmi* (a) or *Te. urticae* (b) observed from leaves in each predator treatment over the duration of the potted tree experiment. Error bars are standard error,  $n = 5$ .

alternative prey that were dependent on each predator, prey species and prey stage combination.

One notable interaction between prey species was competition. On potted trees where no other prey or predator species were present, *P. ulmi* reached a peak density of  $356 \pm 85$  and *Te. urticae* reached a density of  $353 \pm 48$ . The densities of these species were much reduced in treatments where these two prey species were together. In the mixed prey and no predator treatment, peak densities were  $213 \pm 60$  and  $148 \pm 30$  for *P. ulmi* and *Te. urticae*, respectively (Fig. 3). Similarly, alternative prey reduced the density of the primary prey species in the *Ty. pyri* predator treatments. A significant effect of the prey treatment was observed in the repeated-measures ANOVA (Table 2). Post-hoc tests indicated numbers of both prey species were significantly higher in single prey species populations than when an alternative prey species was also present. A significant predator  $\times$  prey interaction term was observed for the analysis of *P. ulmi* numbers. This result indicated that the predators responded differently to the presence of an alternative prey. Examination of the means indicated similar numbers of *P. ulmi* whether or not *Te. urticae* was present in *A. fallacis* treatments (Fig. 4). In *Ty. pyri* and mixed predator treatments, densities of *P. ulmi* were significantly higher when it was alone than when *Te. urticae* was present, and vice versa (Table 2 and Fig. 4).

#### HYPOTHESIS III: THE PREDATOR SPECIES THAT HAS THE HIGHEST MEAN OVIPOSITIONAL RESPONSE WILL OUT-COMPETE THE OTHER PREDATOR SPECIES

As previously noted, *A. fallacis* had a higher ovipositional response than *Ty. pyri* (Figs 1 and 2). An indication of the difference in oviposition between predators

could be observed in the average ratio of *A. fallacis* : *Ty. pyri* oviposition rates at the highest prey densities. On a diet of eggs, *A. fallacis* produced an average of 5.4 times more eggs per day than *Ty. pyri*. On a diet of deutonymphs, *A. fallacis* produced an average of 1.9 times more eggs per day than *Ty. pyri*. We could thus hypothesize that *A. fallacis* would reach higher densities on plants than *Ty. pyri*.

Differences in predator population growth rates should have been most apparent in the first weeks of the potted tree experiments, when the predator : prey ratio was lowest. Interestingly, the highest growth rate observed during this time was by *Ty. pyri* in the mixed prey treatment, which was significantly higher than for *Ty. pyri* in other prey treatments. The repeated-measures ANOVA indicated that all predator treatments had similar densities of predators throughout the experiment (Table 5). However, a significant effect of prey treatment was observed on the predator densities. The lowest number of predators was observed in the *Te. urticae* treatment, while the highest was observed in the treatment with both prey species. No significant repeated-measures effect was observed in this ANOVA. However, a significant prey  $\times$  time interaction occurred as a result of there being relatively constant densities of predators in the treatment with both prey species, but in the *Te. urticae*-only treatment predators took 2–3 weeks to reach similarly high densities.

At the end of the potted tree experiment all the leaves of the apple trees in the mixed predator treatments were picked and the predators were identified. In the mixed predator and *P. ulmi* treatment, 95% of the predators sampled were found to be *Ty. pyri* and 5% were *A. fallacis* ( $n = 150$ ). In the mixed predator and *Te. urticae* treatment, 54% of the predators were *Ty. pyri* and 46% were *A. fallacis* ( $n = 37$ ). In the mixed predator and mixed prey treatment, 80% were *Ty. pyri* and 20% were

**Table 5.** Two-factor repeated-measures ANOVA examining differences in the predator densities in the potted tree experiment. Prey (for the *P. ulmi* model): either *P. ulmi* alone or together with the same density of *Te. urticae*. Prey (for the *Te. urticae* model): either *Te. urticae* alone or together with the same density of *P. ulmi*. Predator treatments: no predator, *A. fallacis*, *Ty. pyri*, or both predators together. Significance of *F* statistics: \**P* < 0.05, \*\**P* < 0.01

| Source of variation    | d.f. (effect) | MS (effect) | <i>F</i> -statistic | Tukey test ( <i>P</i> < 0.05) (Tukey test means in parentheses)   |
|------------------------|---------------|-------------|---------------------|---|
| Predator               | 2             | 0.19        | 0.93                | <i>Ty. pyri</i> (2.23) = <i>A. fallacis</i> (3.04) = both (3.21)  |
| Prey                   | 2             | 1.05        | 5.45**              | <i>Te. urticae</i> (1.67) < both (3.63), <i>P. ulmi</i> (3.19) = both (3.63), <i>Te. urticae</i> (1.67) < <i>P. ulmi</i> (3.19) |
| Predator × prey        | 3             | 0.18        | 0.91                |   |
| Time                   | 4             | 0.17        | 1.93                |   |
| Predator × time        | 8             | 0.09        | 1.72                |   |
| Prey × time            | 8             | 0.23        | 2.62*               |   |
| Predator × prey × time | 16            | 0.07        | 1.47                |   |

*A. fallacis* (*n* = 20). All phytoseiids sampled in the individual predator species treatment were found to be of the species that was initially released, with no evidence of contamination from the other treatments. Unfortunately, due to the low sample sizes of predators from each tree, statistical comparison of species composition between treatments was not possible.

These results offer evidence that contradicts the hypothesis that the predator species with the highest ovipositional response will out-compete the other predator.

## Discussion

How valuable were the functional and numerical responses in determining the best predator for biological control? In our studies, the functional responses of the predators were similar, with the exception of some predator and prey combinations such as *Ty. pyri* and *Te. urticae* eggs. However, *A. fallacis* had an ovipositional response almost twice as high as *Ty. pyri* on three of the four prey items examined. We hypothesized that this higher oviposition rate of *A. fallacis* would mean a faster population growth of this species on potted trees, but this was not observed in practice. Rather, the highest predator population growth rate was observed in one of the *Ty. pyri* treatments. Further complicating matters, although *Ty. pyri* had the highest population growth rate in one of the treatments, in another prey treatment it had the lowest growth rate observed. However, overall, the total number of prey observed was statistically similar in the different prey treatments, irrespective of the predator species. Functional and ovipositional responses alone were thus not informative for predicting the most efficient predator for biological control.

The total response of a predator species includes the functional and numerical responses, the predator migration rate in response to its own densities, interference between predators in foraging, and a developmental response (Price 1997). We examined only the functional and numerical responses. The three other factors may have played a role in the predator dynamics and prey regulation on the potted trees. The growth

rate of *A. fallacis* populations and its final population densities were observed to be statistically similar irrespective of prey treatment. Food was not limiting (at least in the first weeks when growth rates were measured) and *A. fallacis* thus appeared to be regulating its own population growth and densities by some process. This process could be something as simple as successful recruitment, or a more complex process such as density-dependent dispersal (Aars & Ims 2000). However, the growth rate and population dynamics of *Ty. pyri* were significantly influenced by prey treatments. On trees where *Te. urticae* was the only prey, population growth rates and final densities of this species were significantly reduced compared with the other prey treatments. The reduced growth rate of *Ty. pyri* populations in the *Te. urticae* treatment seems unlikely to be related to any of the factors described in the total response. Instead, this result may be related to changes in the ability of *Ty. pyri* to attack different prey species throughout its life history.

When *Ty. pyri* attacked *Te. urticae* eggs, predation on the eggs was incomplete. The eggs were killed, but only a small fraction (if any) of the contents were consumed. The numerical response of *Ty. pyri* on a diet of *Te. urticae* eggs was almost nil. This result suggested that *Te. urticae* eggs contributed little to the nutrition of *Ty. pyri*. Adult *Ty. pyri* may be unaffected by an inability to consume eggs because they can attack other *Te. urticae* stages such as deutonymphs. However, juvenile *Ty. pyri* may not be able to feed on mobile *Te. urticae* stages and could have been limited to consuming nutritionally poor eggs. Such changes in a predator's ability to consume prey during different stages of its life are apparent in other ecological systems (Mol 1996; Cisneros & Rosenheim 1997). Murdoch (1971) recognized that predators change their feeding patterns as they grow, but did not include this factor as part of the developmental response. We feel an inability of juvenile *Ty. pyri* to gain sufficient nutrients from *Te. urticae* populations probably contributed to the low population growth of this predator. Generally, to be a successful biological control agent, sufficient nutrition must be gained from a prey population during the entire life history of a predator species. A predator stage that cannot gain

nutrition from a prey population can thus be considered the weak link in the food chain. This situation may be alleviated should there be alternative prey available to any weak-link stage. Situations where weak links arise are likely to be in food webs with low ecological diversity, such as in agricultural systems (Stoate *et al.* 2001). In such systems, an examination of predation by multiple predator stages is likely to be especially important when examining potential biological control agents.

In the *Ty. pyri* and *Te. urticae* treatment, however, the biological control observed was similar to the other treatments. Despite the low population densities and growth rate of *Ty. pyri*, this predator was able to control *Te. urticae*. This result is consistent with the functional response assay, in which it maintained a high attack rate even in the presence of nutritionally superior *P. ulmi* eggs. This high attack rate of *Ty. pyri* on *Te. urticae* eggs can be considered prey wastage and has been observed in other populations. For example, coyotes *Canis latrans* appear to kill more snowshoe hares *Lepus americanus* than they energetically require or cache (O'Donoghue *et al.* 1998). Similarly, dragonfly *Lestes disjunctus* and *Coenagrion resolutum* larvae may kill many prey but consume less than 50% of these (Krishnaraj & Pritchard 1995). Adult *Ty. pyri* on the potted trees may have similarly continued their attack of *Te. urticae* eggs despite their low nutritional value. This high attack rate effectively controlled *Te. urticae*. Over a longer time period than the duration of the potted tree experiment, *Ty. pyri* would need other prey species for long-term persistence, as its populations would collapse without sustained recruitment.

That *Ty. pyri* continued its attack on *Te. urticae* even in the presence of another prey species is an interesting result of alternative prey. We found evidence that alternative prey occasionally reduced the functional response of the predators, but this was dependent on the predator and prey treatment. The effects of alternative prey on predation were complex and specific to each prey stage, prey species and predator. For example, with the primary prey being *P. ulmi* eggs, *Ty. pyri*'s functional response was not reduced in the presence of alternative prey. However, with the primary prey as *P. ulmi* deutonymphs, a significant reduction in prey consumption was observed as a result of alternative prey. These results clearly make it difficult to generalize about the effects of alternative prey on predation, and especially so when considering different prey stages. No strong switching response was observed, where at high prey densities one prey species is not consumed due to a predator's preference for another prey species. Some generalist predators will completely stop feeding on one prey species in the presence of high densities of an alternative prey (Foglar, Malausa & Wajnberg 1990). Murdoch (1969) suggested prey switching will not occur where strong preferences exist. It seems likely that strong preferences were not apparent with these predator and prey combinations. The only preference

observed was a slight preference by both predators for *Te. urticae* deutonymphs over those of *P. ulmi*. This preference did reduce the functional response of the predators to *P. ulmi*. In the natural environment, the functional response may be further reduced by the presence of a variety of other food sources, including pollen (Wei & Walde 1997).

The most striking effect of alternative prey, however, was between prey species themselves. The density of both prey species while alone was approximately twice that of when they were together, apparently due to interspecific competition (Jeffries & Lawton 1984). Such competition must contribute to the structuring of mite communities in orchards, particularly in orchards that are heavily treated with pesticides, which commonly eliminate many mite predators (Lester, Thistlewood & Harmsen 1998).

In treatments with predators, the predators reacted differently to alternative prey. In the *A. fallacis* treatments, no change in the total number of each prey species was observed when the other prey was present. The total number of each prey species was approximately a quarter of that observed when no predators were present. These results suggest a top-down form of prey regulation, which excluded competitive interactions between prey. In *Ty. pyri* treatments, when both prey were together, prey numbers were a third to a half that observed when each prey species was alone on the potted trees with *Ty. pyri*. At face value, this result appears to suggest some competition between the prey species in mixed prey treatments with *Ty. pyri*. While we cannot exclude the possibility of such competition, *Ty. pyri* also had the highest population growth rate of all prey treatments in the mixed prey treatment. The high abundance and growth rate of *Ty. pyri* in this treatment, relative to the other treatments where each prey species was alone with *Ty. pyri*, may have been the sole factor resulting in the comparatively reduced abundance of prey in the mixed prey and *Ty. pyri* treatments. A diverse diet can result in increased predator recruitment in other systems (Baltz *et al.* 1998; Croxall, Reid & Prince 1999). The effects of prey diversity on a predator are increasingly limited with increasingly specialized predators (Rubega & Inouye 1994). A severe limitation of functional and numerical response analyses is that they do not examine the response of the predator to the true diversity of prey available to a predator in nature. As shown in our study with *Ty. pyri*, the diversity of prey can have dramatic effects on predator population growth and abundance.

Our third hypothesis was that the predator species that has the highest mean ovipositional response will out-compete the other predator species. In mixed predator populations, experiments were initiated with 50% *A. fallacis* and 50% *Ty. pyri*; 5 weeks later in the *P. ulmi* treatment, 95% of the predators were *Ty. pyri*. In the treatment with both predators and both prey, at the end of the study 80% of the predators were *Ty. pyri*. It was only in the treatment with *Te. urticae* as the sole prey

species that *A. fallacis* maintained the approximate ratio at which it was introduced (54% *Ty. pyri* and 46% *A. fallacis*). Thus, predator species composition at the end of the study appeared prey-treatment specific. The abundance of each species in the treatments is likely to be a result of the predator's rate of oviposition, development, survival and interactions within and between predator species. Of the two predators, we observed *A. fallacis* to have the higher oviposition rate. The developmental rate is faster for *A. fallacis* than for *Ty. pyri* (4.9 vs. 7.3 days, at 25 °C), while the survival rate is similar (Zhang & Croft 1994). Predators may regulate their own densities. A predator's per capita death rate can increase with increasing predator density (Abrams & Matsuda 1996). However, such intraspecies interactions are unlikely to explain differences in the abundance of the predators in the mixed predator treatments. These differences are more likely to be explained by interspecies interactions. There may be some intraguild predation occurring between *Ty. pyri* and *A. fallacis*. Croft, Kim & Kim (1996) found that *A. fallacis* was readily consumed by *Ty. pyri*, but *A. fallacis* predated on *Ty. pyri* much less often. The intraguild effects appeared to have greater influence in treatments such as the *P. ulmi* where *Ty. pyri* almost excluded *A. fallacis* populations, rather than the *Te. urticae* treatment.

The results from a recent field experiment confirm many of the results observed in this study. Marshall & Lester (2001) worked in a vineyard with high *P. ulmi* densities where the only naturally occurring predator was *A. fallacis*, although populations of *Ty. pyri* were added to experimental plots in the vineyard. In treatments with *Ty. pyri* releases, *A. fallacis* and *P. ulmi* populations were significantly reduced for successive seasons, compared with control treatments. *Typhlodromus pyri* thus appeared to exclude *A. fallacis* by some mechanism. Of the two predators, *Ty. pyri* was more effective for *P. ulmi* biological control, probably because it was present on the vines early in the season (Marshall & Lester 2001). These results corroborate our experimental studies with the two predators together on apple trees in the laboratory. However, they also highlight further differences between predator species, as differences between predators in the time they were present on the vines were likely to have influenced predator and prey dynamics.

In conclusion, the functional and ovipositional responses, and the effects of alternative prey on these, were of little predictive value in determining the more effective predator for biological control in this study. At most, the responses indicated that these predators would consume both prey species. But even within one prey species, very different results were observed by examining more than one prey stage. These responses did not provide us with information about changes in the ability of predators to consume prey throughout their life history, a clear picture of population growth rates in a mixed population on potted trees, or how predator species would interact. Such processes

resulted in our inability to predict correctly population dynamics in our controlled environment from only the functional and numerical responses. These results confirm a recent study suggesting that laboratory-derived functional responses are of limited use in predicting the impact of predators in field conditions (O'Neil 1997). Further, other results from our field releases of *Ty. pyri* into natural populations of *P. ulmi* and *A. fallacis* indicate that temporal and spatial processes further complicate predator dynamics and biological control (Marshall & Lester 2001). With such inter- and intraguild interactions, perhaps it is no wonder that so many predators fail to establish (Stiling 1993).

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