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Intraguild predation and feeding preferences in three species of phytoseiid mite used for biological control

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Abstract. The ecological impact of introduced biological control agents on native species of arthropods is a matter of considerable debate. This study investigated the ability of the non-native predatory mite *Neoseiulus californicus* to feed on the native *Typhlodromus pyri* and vice versa, as both species now co-occur in UK orchards. *Typhlodromips montdorensis* is a candidate for introduction into the UK as a glasshouse biological control agent. The ability of *T. montdorensis* to feed on the widely used *N. californicus* was investigated to identify possible intraguild predation, which might influence the effectiveness of either or both species as predators of *Tetranychus urticae*. Both *N. californicus* and *T. pyri* consumed larval stages of each other, but in choice experiments both showed a preference for *T. urticae*. Both *N. californicus* and *T. montdorensis* also fed on each other, but whereas *N. californicus* again showed a preference for *T. urticae*, *T. montdorensis* fed equally on *T. urticae* and *N. californicus*. Interactions between *N. californicus* and *T. pyri* and *N. californicus* and *T. montdorensis* are discussed in relation to their effectiveness as biological control agents in the glasshouse and the natural control of spider mite in the field.

Introduction

Evidence suggests that a combination of predation and competition between phytoseiid mites can lead to the displacement of a species from an orchard or other field environments (Yao and Chant 1989; Zhang and Croft 1995; MacRae and Croft 1997; Schausberger 1997). Intraguild predation (IGP) is apparent when two species feed on the same prey and therefore may predate each other (Rosenheim et al. 1995), and is a widespread phenomenon among arthropod food webs (Polis et al. 1989). Such predation can involve one species being the intraguild predator and the other intraguild prey or each species can prey upon the other (Polis et al. 1989; Rosenheim et al. 1995; Holt and Polis 1997). In a biological control context two separate predators may complement each other thereby increasing control of the prey (Losey and Denno 1998; Onzo et al. 2004). In contrast, IGP may cause interference between the two predators and predation of the prey may decrease (Rosenheim 2001). Food shortage can increase IGP (Polis et al. 1989) and this may lead to one of the involved species being out competed and removed from the system (Yao and Chant 1989).

Neoseiulus californicus (McGregor) (Acari: Phytoseiidae) has established outside the glasshouse environment in several areas in the south east and west of England (Jolly 2000) since it was first released under licence as a biological control agent in the UK in 1991. It has generally been found on strawberries and hops but also sighted on apples (Fitzgerald, pers comm). The 'wild' UK strain of *N. californicus* is able to enter diapause outside the glasshouse (Jolly 2000; Hart et al. 2002) and studies on its thermal biology suggest that it is able to survive a 'typical' UK winter (Hart et al. 2002). It is therefore possible that *N. californicus* may become more common in UK orchards and other fruit growing areas.

The most abundant predatory mite in UK apple orchards is the native *Typhlodromus pyri* (Scheuten) (Acari: Phytoseiidae) (Fitzgerald and Solomon 2002). It successfully controls the European red mite, *Panonychus ulmi* (Koch) (Acari: Tetranychidae), where organophosphorous resistant strains of the predator are used in biological control (Solomon et al. 1993, 2000). During sampling from 1997 to 2000, *N. californicus* was found in several areas of the south east and west of England. In most of these cases, *T. pyri* was found at the same sites (Jolly 2001). It was considered important to investigate how *T. pyri* and *N. californicus* may interact in the laboratory and relate these findings to interactions that may occur in the field.

Typhlodromips montdorensis (Schicha) (Acari: Phytoseiidae) was first described in 1978 from New Caledonia and then also reported in Queensland (Australia), Fiji and Tahiti (Schicha 1979). It is reported to feed on eriophyid mites, *Tetranychus urticae* (Koch) (Acari: Tetranychidae) (Schicha 1979), broad mite, tomato russet mite and other small arthropods (Steiner and Goodwin 2002a), on common bean, strawberry, cucumber and tomato. In Australia *T. montdorensis* is being marketed as a field biological control agent of thrips such as Western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) and onion thrips *Thrips tabaci* (Lindeman) (Thysanoptera: Thripidae) on cucumber and strawberries (Steiner 2002; Steiner and Goodwin 2002b). It has recently been demonstrated that *T. montdorensis* is unlikely to establish outside the glasshouse environment in the UK (Hatherly et al. 2004, 2005). It is therefore likely that *T. montdorensis* will be licensed for release in the UK. If this is the case, growers may introduce the species into glasshouses with the widely used *N. californicus*. It was therefore of interest to determine whether *T. montdorensis* and *N. californicus* would feed on each other, as IGP may cause interference between both species and decrease the control of *T. urticae* in a glasshouse biological control programme. Alternatively, IGP as a result of prey shortage, may lead to a stabilisation of the predator population levels (Polis et al. 1989) and decrease the need for continual release of the predators when the density of low *T. urticae* is low.

In this study comparisons of prey consumption, longevity and fecundity of each mite species were made to help identify possible interactions in the field (for *N. californicus* and *T. pyri*) and in the glasshouse (for *N. californicus* and *T. montdorensis*).

Materials and methods

Mite rearing

Neoseiulus californicus and *T. montdorensis* were obtained from Syngenta Bioline, Essex, UK and *T. pyri* was cultured from individuals provided by HRI, West Malling, Kent, UK. Stock cultures of the three species were fed with *T. urticae* and cattail pollen (Typha species) and reared at 25 °C, 18:6 LD. The culturing method was adapted from Overmeer (1985). Mites were placed on black ceramic tiles (13×17×0.8 cm), on a sponge block (6×14×4 cm) submerged in water in a plastic box (17×25×9 cm). OecoTak® A5 (Oecos, Hertfordshire, UK), a non-drip insect trapping adhesive, was applied to the outer edge of the tiles and provided a physical barrier for the mites. A 0.5 cm wide, 10 cm long piece of cotton wool connected the tile to the water as a moisture source. Lids with holes (14×8 cm) covered in muslin were placed on the plastic boxes. Strands of cotton thread (2 cm long) frayed at both ends provided an oviposition site for the females (Hatherly et al. 2004).

Experimental set-up

To determine whether *N. californicus* would feed on *T. montdorensis* and *T. pyri* and whether *T. montdorensis* and *T. pyri* would feed on *N. californicus* the initial sequence of experiments involved a no-choice design, i.e. an adult mite was provided with only the larval stages of its phytoseiid prey. As a control, adults of each species were fed solely on *T. urticae* larvae. The second set of experiments presented adult mites of each species with 50% *T. urticae* and 50% of larval phytoseiid as a food source (choice test). Larvae were the selected food source as studies have demonstrated the importance of immature stages, particularly larvae, as prey for phytoseiids when their target food (*T. urticae*) is unavailable in the field (Croft and MacRae 1992; Croft et al. 1992). Additionally, larvae were easy to handle and could be quickly selected once they had hatched. All *T. urticae* used as prey were mixed first and second instar.

One adult male and one adult female (7 days after hatching) of each species (22 pairs in total for each species) reared at 25 °C, were transferred onto on individual rearing arenas (Hatherly et al. 2004) at 22 °C, 18:6 LD with excess food and left to mate. After 24 h the male was removed and the female was transferred to a fresh arena without food and left for a further 24 h to ensure that all individuals had been starved for an equal period of time. A 1 cm long piece of black cotton thread frayed at one end was placed on each arena for oviposition. Each treatment (Table 1) consisted of 22 mated females on individual arenas supplied with a specific prey species. The exception was treatments with adults on 16 *T. urticae* and 16 phytoseiid larvae only had 12 mated females. This treatment was included as when fed 8 *T. urticae* and 8 phytoseiid larvae, adults were sometimes eating up to 7 *T. urticae*. Therefore, by increasing the number of prey, it was hoped that the possibility of attacks on less preferred prey (thereby obscuring prey preference), would be avoided.

Every 24 h the number of eggs laid, the number of each food source consumed (determined by larval carcasses), and whether the female was alive or dead, was recorded. All excess food and carcasses on the arenas were removed at each observation period and replaced with an identical amount of food as previously supplied. This procedure was repeated until the female had died. Oviposition rate, longevity and prey consumption was recorded for each female of each species. For treatments consisting of two prey sources, the ratio of the number of *T. urticae* eaten compared with the number of phytoseiid larval prey consumed was determined.

The mean longevity, mean number of eggs laid per female per day, total eggs per female, mean number of prey consumed per female per day and total prey consumed per female were analysed by a One-way ANOVA for each species kept on each of its prey sources. Differences between treatments were compared by Tukey's HSD. The longevity data was log transformed to ensure a normal distribution. Each of the three species were fed on 16 *T. urticae* and these were the only treatments that allowed direct comparison, as there was always the same prey source. As *N. californicus*, *T. montdorensis* and *T. pyri* fed on 16 *T. urticae* were used in multiple comparisons a Bonferroni correction (Legendre and Legendre 1998) was applied to control for elevated type 1 errors where applicable. All statistical analyses were done in MINITAB version 14 (Minitab Inc., State College, Pennsylvania).

To ensure that larvae of the predators were not feeding during experiments, 22 replicates of each combination of prey and predator used were set up

Table 1. Number of *Neoseiulus californicus* (N.c), *Typhlodromips montdorensis* (T.m) and *Typhlodromus pyri* (T.p) larvae recovered alive (%), number recorded in OecoTac® (%), number eaten (%) and number dying of natural causes (%) after 24 h during combinations of either phytoseiid larvae alone or with *Tetranychus urticae* (T.u).

Larvae	% Recovered alive	% In OecoTak®	% Eaten	% Dead by natural causes
8 N.c	90	7	0	3
8 T.m & 8 T.u	94 & 89	5 & 8	0 & 2	1 & 1
8 T.p & 8 T.u	83 & 75	12 & 17	1 & 3	4 & 3
8 T.m	95	3	0	2
8 N.c & 8 T.u	92 & 93	3 & 2	0 & 0	5 & 5
8 T.p	90	7	0	3
8 N.c & 8 T.u	86 & 88	11 & 10	0 & 0	3 & 2

without the adults and left for 24 h and then checked for larval mortality. Larvae that had died of natural causes were slightly desiccated but whole individuals. Larvae that had been predated by other larvae were found as shrivelled carcasses. Some larvae were detected dead within the OecoTak® barrier.

Results

The results for the control experiments are given in Table 1. For ease of comparison, ease all other results are collated in Table 2. As the results for mixed diets of 8 or 16 *T. urticae* and 8 or 16 phytoseiid larvae were not significantly different to any of the other treatments, all comments regarding mixed diets in the results and discussion refer to both prey densities.

Controls

With one exception (8 *T. pyri* with 8 *T. urticae*) in excess of 80% of all control larvae were recovered. Up to 17% were found in the OecoTak® but during the experiments with adults, any larvae found in the sticky barrier were discounted. Up to 5% of some larvae died within 24 h. Their appearance suggested this was not due to predation by other larvae. Only in three cases were any larvae recorded as dead from attacks by other individuals.

Performance of phytoseiid mites with Tetranychus urticae *as the sole prey source*

Neoseiulus californicus and *T. pyri* survived significantly longer than *T. montdorensis* ($F_{2,63} = 9.82$, $p < 0.01$ and $F_{2,63} = 3.3$, $p < 0.05$ respectively). *Neoseiulus californicus* and *T. montdorensis* both laid significantly more eggs per female per day than *T. pyri* when fed solely on *T. urticae* ($F_{2,127} = 3.29$, $p < 0.05$). Equally this applied to total egg production ($F_{2,127} = 9.82$, $p < 0.01$). There were no significant differences in the mean number of prey eaten per day or the total number of prey consumed by the three species ($F_{2,127} = 0.66$, $p > 0.05$ and $F_{2,127} = 1.42$, $p > 0.05$).

Performance of Neoseiulus californicus *with either* Typhlodromus pyri *or* Typhlodromips montdorensis *as prey*

Neoseiulus californicus survived significantly longer when fed on *T. urticae* alone than when fed either on a mixed diet of *T. urticae* and *T. pyri*, or solely on *T. pyri* ($F_{2,63} = 33.2$, $p < 0.01$). Using a mixture of *T. urticae* and *T. pyri* gave a higher mean oviposition rate per day by *N. californicus* than when fed

Table 2. Mean (±SE) longevity, mean number (±SE) of eggs laid per female per day, total number (±SE) of eggs laid per female, mean number (±SE) of prey consumed per female per day and total number (±SE) of prey consumed per female for *Neoseiulus californicus* (N.c), *Typhlodromips montdorensis* (T.m) and *Typhlodromus pyri* (T.p) fed solely on *Tetranychus urticae* (T.u) or on a combination of *T. urticae* and larval phytoseiid.

Predator	Prey and number	Mean longevity (days ± SE)	Mean eggs (±SE) per female per day for lifetime	Total eggs (±SE) per female	Mean number of prey (±SE) consumed per female, per day	Total prey (±SE) consumed per female	Ratio of T.u:predator larvae consumed
N.c	16 T.u	27.9 ± 2.8a	0.62 ± 0.18a	31.6 ± 2.4a	2.8 ± 0.60a	144 ± 9.0a	n/a
N.c	8 T.u & 8 T.p	11.1 ± 0.9b	1.20 ± 0.12b	20.6 ± 2.2b	4.2 ± 0.46a	73 ± 6.6b	2.2:1
N.c	16 T.p	10.3 ± 1.0b	0.66 ± 0.15a	12.6 ± 1.4c	2.4 ± 0.42a	45 ± 3.7c	n/a
N.c	16 T.u & 16 T.p	13 ± 1.3b	1.40 ± 0.33b	22 ± 2.6b	4.4 ± 0.5a	71 ± 7.0b	2.1:1
N.c	8 T.u & 8 T.m	21.2 ± 2.0ab	0.61 ± 0.12a	24.5 ± 2.1ab	3.4 ± 0.56a	138 ± 11a	2.6:1
N.c	16 T.m	16.0 ± 1.9b	0.48 ± 0.14a	21.7 ± 2.0b	1.6 ± 0.43b	70 ± 6.7b	n/a
N.c	16 T.u & 16 T.m	22.4 ± 2.5ab	0.68 ± 0.22a	25.5 ± 2.9ab	3.7 ± 0.56a	125 ± 9.5a	2.5:1
T.m	16 T.u	15.0 ± 1.6a	0.68 ± 0.15a	22.5 ± 2.1a	3.5 ± 0.68a	114 ± 11a	n/a
T.m	8 T.u & 8 N.c	8.8 ± 0.6b	0.60 ± 0.13a	12.5 ± 1.3b	3.4 ± 0.72a	70 ± 4.9b	1:1
T.m	16 N.c	10.3 ± 0.7b	0.80 ± 0.16a	16.7 ± 1.3ab	3.9 ± 0.72a	82 ± 6.8b	n/a
T.m	16 T.u & 16 N.c	10.0 ± 2.0b	0.65 ± 0.21a	13.5 ± 1.8b	4.0 ± 0.98a	78 ± 5.2b	1.1:1
T.p	16 T.u	21.5 ± 2.3a	0.32 ± 0.09a	14.8 ± 1.5a	2.7 ± 0.65a	125 ± 9.1a	n/a
T.p	8 T.u & 8 N.c	18.5 ± 1.3a	0.46 ± 0.07a	13.4 ± 1.3a	3.0 ± 0.44a	88 ± 6.5a	2.8:1
T.p	16 N.c	21.3 ± 1.9a	0.30 ± 0.07a	12.6 ± 1.9a	1.4 ± 0.23b	57 ± 7.3c	n/a
T.p	16 T.u & 16 N.c	20.7 ± 2.4a	0.40 ± 0.17a	11.4 ± 1.5a	3.4 ± 0.82a	89 ± 9.2b	3.2:1

Where applicable the ratio of *T. urticae* to larval phytoseiids consumed by adult predators is given. Values in each column followed by the same letter are not significantly different ($p > 0.05$) when predators fed on 16 *T. urticae* are compared to their other three prey combinations.

T. pyri or *T. urticae* alone ($F_{2,84} = 4.08$, $p < 0.05$). *Neoseiulus californicus* fed *T. urticae* laid more eggs in total than *N. californicus* fed on a mixed diet and the least eggs were laid by *N. californicus* fed solely on *T. pyri* ($F_{2,63} = 21.1$, $p < 0.01$). Prey type or number did not influence the number of prey consumed per day by *N. californicus* ($F_{2,84} = 2.87$, $p > 0.05$), however *N. californicus* fed *T. urticae* consumed more prey in total than *N. californicus* fed on a mixed diet and the least prey was eaten by *N. californicus* fed solely on *T. pyri* ($F_{2,63} = 50.3$, $p < 0.01$). *Neoseiulus californicus* consumed up to 2.2 *T. urticae* for every 1 *T. pyri* when fed on both prey sources.

Neoseiulus californicus survived significantly longer when fed on *T. urticae* alone or on a mixture of *T. urticae* and *T. montdorensis* than when fed only on *T. montdorensis* ($F_{2,63} = 6.97$, $p < 0.01$). Prey type or number did not affect the number of eggs laid by *N. californicus* females per day ($F_{2,133} = 0.54$, $p > 0.05$). In contrast the total egg production of *N. californicus* was higher when fed on *T. urticae* or on a mixed diet of *T. urticae* and *T. montdorensis* than when preying on *T. montdorensis* ($F_{2,63} = 4.89$, $p < 0.05$). *Neoseiulus californicus* fed *T. urticae* consumed more prey per day and in total than *N. californicus* fed solely on *T. montdorensis* ($F_{2,133} = 6.31$, $p < 0.01$ and $F_{2,63} = 19.89$, $p < 0.01$, respectively). *Neoseiulus californicus* consumed up to 2.6 *T. urticae* for every 1 *T. montdorensis* when fed on both prey sources.

Performance of Typhlodromips montdorensis *and* Typhlodromus pyri *with* Neoseiulus californicus *larvae and/or* Tetranychus urticae *as prey*

Typhlodromips montdorensis survived significantly longer when fed exclusively on *T. urticae* than when fed on a mixed diet of *T. urticae* and *N. californicus* or when fed only on *N. californicus* ($F_{2,63} = 7.8$, $p < 0.01$). Prey type did not affect the mean number of eggs laid per day ($F_{2,66} = 0.43$, $p > 0.05$), however when fed *T. urticae* or *N. californicus* total oviposition was higher than when fed on a mixed diet ($F_{2,63} = 9.26$, $p < 0.01$). Prey type or number did not affect the mean number of prey eaten per day by *T. montdorensis* ($F_{2,66} = 1.0$, $p > 0.05$), but in total *T. montdorensis* fed *T. urticae* consumed more prey than when fed a mixed diet or solely on *N. californicus* ($F_{2,63} = 6.31$, $p < 0.01$). *Typhlodromips montdorensis* consumed up to 1.1 *T. urticae* for every 1 *N. californicus* when fed on both prey sources.

Prey type or number did not affect the longevity ($F_{2,63} = 0.3$, $p > 0.05$), the mean number of eggs laid ($F_{2,114} = 1.79$, $p > 0.05$) or the total number of eggs laid by *T. pyri* ($F_{2,63} = 0.72$, $p > 0.05$). *Typhlodromus pyri* consumed the least prey per day when fed only on *N. californicus* ($F_{2,114} = 5.87$, $p < 0.01$) and when fed a mixed diet or solely *N. californicus* the total prey consumption was less than when fed on *T. urticae* ($F_{2,63} = 19.13$, $p < 0.01$). *Typhlodromus pyri* consumed up to 3.2 *T. urticae* for every 1 *N. californicus* when fed on both prey sources.

Discussion

During the control experiments a maximum of only 3% of *T. urticae* were eaten by predatory larvae. Only 1% of *T. pyri* larvae were cannibalised by other *T. pyri* and no *N. californicus* or *T. montdorensis* larvae were fed on. Other studies on *T. pyri* have revealed that its larvae do not feed (Hayes and McArdle 1987; Croft and Croft 1993) and *N. californicus* larvae have only been reported to feed very little (Monetti and Croft 1997) and are able to moult to the protonymphs.

The present study shows that *N. californicus* can feed on larval stages of *T. montdorensis*; however total fecundity and longevity are reduced when compared with *N. californicus* fed solely on *T. urticae*. Prey consumption is lower when *T. montdorensis* is the only food source but, there was no difference in the number of eggs laid per day by *N. californicus* fed on *T. urticae* or fed on *T. montdorensis* and therefore *T. montdorensis* may be a more nutritional food source than *T. urticae*. Nevertheless, when presented with a mixed diet, *N. californicus* showed a marked preference for *T. urticae*, suggesting that it is its preferred food. It is likely that *N. californicus* can develop and reproduce when fed exclusively on *T. montdorensis* for a limited period of time but, if no other prey becomes available, it may lose some of its effectiveness as a biological control agent in the glasshouse due to reduced longevity and total prey consumption. *Typhlodromips montdorensis* survived longest when fed solely on *T. urticae*. In the mixed diet choice experiments, *T. montdorensis* showed no preference for *T. urticae* over *N. californicus* and this may help explain why there were no differences in performance between *T. montdorensis* fed on a mixed diet or *N. californicus* alone.

Concurrent releases of *N. californicus* and *T. montdorensis* in the same glasshouse may to lead to co-existence of the two generalist species. Intraguild predation is particularly common in a generalist species as they will often consume other natural enemies as well as the target pest (Janssen et al. 1998). As *N. californicus* shows a preference for *T. urticae* it is likely to feed primarily on this species, but at the beginning and the end of the cropping season, when *T. urticae* is in short supply, it may be able to feed on *T. montdorensis* to maintain its population for a short time. This may stabilise the *N. californicus* population levels over time (Polis et al. 1989). In contrast, *T. montdorensis* shows no preference for *T. urticae* and is therefore likely to be less selective in its food source but, longevity and correspondingly total fecundity and prey consumption was highest with *T. urticae* as the sole prey. From a biological control perspective, it would be beneficial to release a generalist predator such as *N. californicus* and a more specialised species for example, *Phytoseiulus persimilis* (Athias-Henriot) (Acari: Phytoseiidae). Recent work on the interactions between these species has revealed that they can suppress *T. urticae* effectively when used together (Schausberger and Walzer 2001; Walzer et al. 2001). The specialist is likely to provide effective short term pest suppression and the generalist will have a greater ability to persist at low prey levels, i.e. at the beginning and the end of a cropping season. Only glasshouse trials can effectively determine how the concurrent release of both *N. californicus* and *T. montdorensis* will influence the control of *T. urticae*.

How successfully *N. californicus* and *T. pyri* feed, survive and reproduce on each other in the laboratory may give some indication as to what may happen in the field. This may be of interest from a species composition perspective and for biological control, as *T. pyri* is used as a control agent in apple orchards in the Netherlands, Switzerland and Italy (Blommers 1994). *Typhlodromus pyri* consumed more prey when fed only on *T. urticae*, but there was no difference in fecundity and longevity when fed both *T. urticae* and *N. californicus* or just on the latter prey. Previous work on *T. pyri* and *Metaseiulus occidentalis* (Nesbitt) (Acari: Phytoseiidae) revealed a trend that phytoseiid larvae were less favourable for oviposition than tetranychid larvae. This observation was more marked in *M. occidentalis* than in *T. pyri* (MacRae and Croft 1993, 1997). When fed both *T. urticae* and *T. pyri*, *N. californicus* showed a preference for feeding on *T. urticae*, and *T. pyri* showed an even greater preference to feed on *T. urticae* compared with *N. californicus* when given a mixed diet. In the field in the UK, three to four generations of *T. pyri* are possible each year (Solomon et al. 2000); however for *N. californicus*, six generations a year are theoretically possible (Hart et al. 2002). Therefore, both species are able to reproduce well in the UK climate and may co-occur.

Early and late in the season when prey is not as widely available as during the summer months, the ability of *T. pyri* and *N. californicus* to exploit other prey sources may have an influence on their relative abundance. The ability of both species to utilise phytoseiid prey suggests that they will be able to stabilise their population levels when tetranychid prey is unavailable. *Typhlodromus pyri* can show a clear preference for certain food sources; for example, it prefers *P. ulmi* to apple rust mite, *Aculus schlechtendali* (Nalepa) (Acari: Eriophyidae) (Dicke 1988; Dicke and Dejong 1988), despite development being quicker and reproductive capacity higher on the latter (Dicke et al. 1990). It has been well documented that *N. californicus* (Raworth et al. 1994; Castagnoli et al. 1999, 2001) and *T. pyri* (Dosse 1961; Croft et al. 1992; Walde et al. 1992) can feed on pollen and during the present study both species fed on cattail pollen in culture. When deprived of food *N. californicus* feeds less on its own egg and immature life stages than *T. pyri* (Croft and Croft 1993, 1996). A large number of mite species will benefit more from predating other phytoseiids than from cannibalism (Schausberger and Croft 1999, 2000; Walzer and Schausberger 1999b) as it is likely more nutrients will be gained from such IGP (Schausberger 1997; Walzer and Schausberger 1999a).

There are a large number of predatory mite species present in UK orchards. A recent 5-year survey revealed *T. pyri* was the most abundant but *Phytoseilus macropilis* (Banks) and *Euseius finlandicus* (Oudemans) (Acari: Phytoseiidae) were also common and *Amblyseius andersoni* (Chant), *Paraseiulus soleiger* (Ribaga) and *Kampimodromus aberrans* (Oudemans) (Acari: Phytoseiidae) were locally abundant (Fitzgerald and Solomon 2002). The next long term survey may reveal *N. californicus* as an increasingly abundant species and it will be of interest to see what numbers of *T. pyri* are recorded. At present it is hard to predict how *N. californicus* and *T. pyri* will interact in the field. It is possible, that due to the abundance of phytoseiid mites in UK orchards, all species may be able to co-exist. Recent work in Japan has shown that introductions into Japanese orchards of *Typhlodromus occidentalis* (Nesbitt) (Acari: Phytoseiidae), *T. pyri* and *Neoseiulus fallacis* (Garman) (Acari: Phytoseiidae) from New Zealand did not have any significant impact on native phytoseiids. After a 5–10-year period, only native phytoseiid species were found during sampling at the release sites (Mochizuki et al. 2003, 2004).

In the present study phytoseiid larvae were the selected alternative food source as the importance of immature stages, particularly larvae, as prey for phytoseiids when their primary food (*T. urticae*) is unavailable in the field has been previously demonstrated (Croft and MacRae 1992; Croft et al. 1992). To fully understand IGP between species, all life stages need to be studied. In extreme circumstances IGP may lead to displacement of a species (Yao and Chant 1989; MacRae and Croft 1997); however, it is also possible that IGP may alter the distribution of prey in a given area and lead to a more homogenous distribution of predators (Holt and Polis 1997) which may even enhance biological control. In conclusion, the present study has revealed IGP exists between the three species tested and it is the first step in understanding possible interaction between *N. californicus* and *T. montdorensis* in the glasshouse and between the former and *T. pyri* in UK orchards.

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