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Messelink, G.J.; van Maanen, R.; van Steenpaal, S.E.F.; Janssen, A.

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Biological control of thrips and whiteflies by a shared predator: Two pests are better than one

Gerben J. Messelink [a,*], Roos van Maanen [b], Sebastiaan E.F. van Steenpaal [a], Arne Janssen [b]

[a] *Wageningen UR Greenhouse Horticulture, P.O. Box 20, 2265 ZG Bleiswijk, The Netherlands*
[b] *IBED, Section Population Biology, University of Amsterdam, P.O. Box 94084, 1090 GB Amsterdam, The Netherlands*

Abstract

We studied the capacity of one species of predator to control two major pests of greenhouse crops, Western flower thrips (*Frankliniella occidentalis* (Pergande)) and the greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood)). In such a one-predator–two-prey system, indirect interactions can occur between the two pest species, such as apparent competition and apparent mutualism. Whereas apparent competition is desired because it brings pest levels down, apparent mutualism is not, because it does the opposite. Because apparent competition and apparent mutualism occurs at different time scales, it is important to investigate the effects of a shared natural enemy on biological control on a time scale relevant for crop growth. We evaluated the control efficacy of the predatory mites *Amblyseius swirskii* (Athias-Henriot) and *Euseius ovalis* (Evans) in cucumber crops in greenhouse compartments with only thrips, only whiteflies or both herbivorous insects together. Each of the two predators controlled thrips, but *A. swirskii* reduced thrips densities the most. There was no effect of the presence of whiteflies on thrips densities. Whitefly control by each of the two predators in absence of thrips was not sufficient, yet better with *E. ovalis*. However, whitefly densities in presence of thrips were reduced dramatically, especially by *A. swirskii*. The densities of predators were up to 15 times higher in presence of both pests than in the single-pest treatments. Laboratory experiments with *A. swirskii* suggest that this is due to a higher juvenile survival and developmental rate on a mixed diet. Hence, better control may be achieved not only because of apparent competition, but also through a positive effect of mixed diets on predator population growth. This latter phenomenon deserves more attention in experimental and theoretical work on biological control and apparent competition.
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Keywords: Biological control; *Frankliniella occidentalis*; *Trialeurodes vaporariorum*; Phytoseiidae; *Amblyseius swirskii*; *Euseius ovalis*; Apparent competition; Mixed diet

1. Introduction

The use of different natural enemies for the biological control of different pest species results in the creation of complex artificial food webs in agricultural crops. This implies that pest densities are not only determined by the natural enemies of that pest, but also by direct and indirect interactions with other pests and enemies, and such interactions can affect biological control (Rosenheim et al., 1995; Janssen et al., 1998). The use of one natural enemy to control several pests will result in food webs simpler than those in which different enemies are introduced against each pest species. However, such a natural enemy may mediate indirect interactions between these pest species, which in turn may be beneficial or detrimental to biological control. One such interaction between two pest species through a shared natural enemy is apparent competition, which Holt (1977) defined as the indirect interaction between prey through shared predation. When two prey species share a natural enemy, the equilibrium density of one of the prey species decreases with increasing equilibrium density of the other species.

* Corresponding author. Fax: +31 10 5225193.
  E-mail address: gerben.messelink@wur.nl (G.J. Messelink).

This is because the density of the shared natural enemy increases with the increased equilibrium density of either prey species (Holt, 1977; Müller and Godfray, 1997; Janssen et al., 1998; van Rijn et al., 2002; Morris et al., 2004). This interaction can even lead to exclusion of one of the two prey species (Bonsall and Hassell, 1997).

The addition of alternative food to better suppress a pest species through apparent competition has been used in biological control, often with the desired result (Karban et al., 1994; Hanna et al., 1997; van Rijn et al., 2002; Liu et al., 2006). However, the alternative food often consists of non-prey, such as pollen (van Rijn et al., 2002), or the alternative prey is not a pest, but serves primarily as alternative food to build up predator populations (Karban et al., 1994; Hanna et al., 1997; Liu et al., 2006). Here, we investigate the effects of apparent competition between two prey species that are both serious pests of various crops worldwide.

Two prey species that share a predator may also affect each other's densities positively because an increase in the numbers of one pest species may lead to predator satiation, resulting in decreased predation on the other pest species. In addition, predators may switch to the most abundant prey species, thus releasing the other species from predation. Such positive indirect effects are referred to as apparent mutualism (Holt and Lawton, 1994; Abrams and Matsuda, 1996). Apparent mutualism occurs mostly at a shorter time scale than apparent competition (Harmon and Andow 2004; van Veen et al., 2006). Hence, depending on time-scale and prey preference, a natural enemy that feeds on two pest species can mediate mutualistic or antagonistic interactions between the two pests. The use of one species of natural enemy for biological control of two pests may thus result in reduced control in the short-term, but increased control in the long-term (van Rijn et al., 2002). It is therefore relevant to assess the time scale at which indirect interactions occur. In our system, this scale is set by the length of the growing season of the greenhouse crop.

In the literature on apparent competition, little attention has been given to the effect of mixed diets on the performance of predators. Mixed diets are known to have positive effects on reproduction in some predator species (Wallin et al., 1992; Toft 1995; Evans et al., 1999), and the effect of adding a new prey species would then surpass that of simply adding more prey items with the same nutritive value. Therefore, we also investigated the effects of a mixed diet on predator survival and reproduction.

1.1. The experimental system

Western flower thrips (*Frankliniella occidentalis* (Pergande)) and greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood)) are two major pest species in various crops in Northern Europe and North America (Lewis, 1997; Byrne et al., 1990). The phytoseiid *Amblyseius swirskii* (Athias-Henriot) (Chant and McMurtry, 2004) has

recently been shown capable of suppressing populations of the tobacco whitefly (*Bemisia tabaci* (Gennadius)) (Nomikou et al., 2001; Nomikou et al., 2002). *Euseius ovalis* (Evans), another species of predatory mite, also feeds and reproduces on a diet of *B. tabaci* (Borah and Rai, 1989). An evaluation of phytoseiids for control of Western flower thrips in greenhouse cucumber showed that *A. swirskii* and *E. ovalis*, amongst others, are much more effective thrips predators than *Neoseiulus cucumeris* (Oudemans), a phytoseiid that is often used to control thrips, (Messelink et al., 2005, 2006). Thus, each of the two mites *A. swirskii* and *E. ovalis* can potentially control whiteflies and thrips.

We studied the dynamics of Western flower thrips and greenhouse whiteflies separately as well as together on cucumber plants (cv Aviance RZ) with one of the two predatory mite species in small greenhouse compartments. Cucumber plants have a short cropping season, and short-term effects of shared predation, such as apparent mutualism, may determine the dynamics of the pests and predators. For biological control, it is therefore important to assess whether the effects of shared predation on pest levels are positive or negative. In order to detect an effect of mixed diet on the population dynamics of the predator, we also compared the effect of diets consisting of pest species separately or of a mix of both species on several life-history parameters of *A. swirskii* that are important for population dynamics (oviposition, juvenile survival, development).

2. Materials and methods

2.1. Cultures

For the greenhouse experiments, the predatory mites were reared on flowering *Ricinus communis* L. plants in small greenhouses. The predators fed on the pollen, amply produced by these plants. Western flower thrips were reared on flowering chrysanthemum plants cv. Miramar. The greenhouse whitefly was reared on tobacco plants (*Nicotiana tabacum* L.). Cucumber plants cv. Aviance RZ were grown in rock wool blocks in a greenhouse compartment without any application of pesticides. The greenhouse experiments were carried out at Wageningen UR Greenhouse Horticulture, Naaldwijk, The Netherlands.

For the laboratory experiments, *A. swirskii* mites were reared on plastic arenas (8×15 cm), placed on a wet sponge in a plastic tray containing water (Nomikou et al., 2003a). They were fed cattail pollen, *Typha latifolia* L twice per week. Western flower thrips were reared in climate boxes and greenhouse whiteflies in a walk-in climate room. Their host plants were cucumber plants cv. Aviance RZ, grown from seeds in plastic pots (2 l) with soil and kept in a walk-in climate room, free of herbivores, before use in the arthropod cultures. Laboratory experiments were carried out at the Section Population Biology, University of Amsterdam, The Netherlands.

2.2. Greenhouse experiments

The effects of the predators *A. swirskii* and *E. ovalis* on western flower thrips, greenhouse whitefly and a combination of these two pests was examined in a greenhouse experiment in 12 separate compartments (each 18 m²) that each contained two tables (1 × 3 m) on which cucumber plants were grown. The experiment was set-up as a split-plot experiment with four replicates. Each block contained one compartment with thrips, one compartment with whiteflies and one compartment with thrips and whiteflies. In each compartment, *A. swirskii* was released on plants on one table and *E. ovalis* on the other table. Note that we did not include control treatments in which the pest species had no predators. Hence, we have no data on the effects of the pest species on each other through the shared host plant. The plants in the treatments with both pest species had such low damage levels that exploitative competition between the two pests was improbable, certainly when we consider the large leaf size of a cucumber crop (in this treatment 250–450 cm²). However, the two pests possibly affected each other through induced plant responses (Karban and Carey, 1984). This will be the subject of forthcoming research. Secondly, it should be realized that the predator treatments are strictly not independent, because thrips and whiteflies were able to migrate between the two tables in a compartment. This migration might result in an underestimate of the control capacity of the best performing predator, and an overestimate of the capacity of the other predator. However, for analyzing results we assumed the predator treatments to be statistically independent.

Each greenhouse compartment had a small closed entrance corridor without windows and was equipped with an air pressure system in order to minimize contamination with organisms from outside. Plants were at the fifth-leaf stage when the experiments started, and roots were preventively treated with Propamocarb against *Pythium* spp. Four plants were placed on two pieces of a rock wool substrate slab on each table. The experiment started in week number 12. The rock wool slabs were continuously immersed in a nutrient solution that was automatically supplied once per day. Plants were cultivated vertically up to a 1.5 m high crop supporting wire. Side-shoots were removed until the top of the plant reached the crop supporting wire. Later on, plant shoots and side shoots grew down over the crop supporting wire. Contamination of treatments was avoided by applying insect glue to the wires supporting the crop and by keeping the plants isolated in the water layer on the tables.

Pests were introduced one day after the cucumber plants were planted. Forty adult female thrips, collected from the culture using an aspirator, were released on each table. A total of 120 adult whiteflies were released per table. The population of whiteflies contained on average 42% females. The same numbers were released in the treatment with both pests. Predatory mites were released seven days after introducing the pests. Female predatory mites were sampled with a fine paintbrush in the laboratory and placed on leaf discs of sweet pepper (*Capsicum annuum*) (diameter 2 cm) containing cattail pollen. One leaf disc with 15 mites was introduced on the upper leaves of each cucumber plant.

The experiment lasted 11 weeks. During this period, the crop was inspected twice a week, and cucumbers were harvested as soon as they reached the standard fruit size. Different treatments were handled by different persons to avoid cross-contamination. The treatments with different pests were indeed not invaded by other pests, except for one compartment with whiteflies, which was invaded by spider mites in week 8. This spot was treated by releasing 100 adults of the predatory mite *Phytoseiulus persimilis* (Athias-Henriot), resulting in successful control. *Phytoseiulus persimilis* does not consume thrips or whiteflies, and they were not observed after the spider mites had been eradicated, within a few days. Powdery mildew occurred occasionally during the experiment, but infections remained limited to small spots because the cucumber variety used is partially resistant to mildew.

The numbers of predatory mites and pests were assessed 4, 6, 8 and 10 weeks after introducing the predatory mites. Plants were not sampled during the first 4 weeks in order not to cause disturbance. Assessing the populations was done by collecting six leaves from each treatment by randomly choosing three shoots of which the sixth and eighth leaf from the tip was collected. These leaves were each put in a separate plastic bag and transported to the laboratory where they were cut into strips of 5 cm. The number of mites, thrips and whiteflies were counted on both sides of the leaves using a binocular microscope (40×). All mites were slide-mounted for identification to species, gender and life-stage under a microscope (400×). Only the larval stages of thrips were counted, and eggs, larvae and pupae of whiteflies were counted separately. When densities of whiteflies exceeded 500 individuals per leaf, densities were assessed on part of each leaf only, and extrapolated to the whole leaf. The leaf area of each collected leaf was measured with an optical area meter (LI-COR LI-3100) after mite and pest densities were quantified. The average temperature and relative humidity were comparable for each block treatment (Table 1).

The results were analysed with linear mixed effects models (lme in R), with time as random factor nested in blocks

Table 1
Experimental conditions in the four experimental blocks during the greenhouse experiment

	Block			
	1	2	3	4
Mean temperature (°C)	22.5	22.2	22.8	22.5
Mean relative humidity (%)	74	75.8	76.7	80.5

Each block contained three separate greenhouses with a thrips, whitefly or thrips & whitefly treatment.

to correct for pseudoreplication due to repeated measures (Crawley, 2002). The numbers of thrips and whiteflies were log $(x + 1)$ transformed before the analysis, in order to stabilise variance. Treatments were compared through model simplification by combining treatments (Crawley, 2002).

2.3. Oviposition, juvenile survival and development and predation

The oviposition rate and predation rate of *A. swirskii* was measured during three days on three different diets: whitefly eggs, young first instars thrips and a mixture of whitefly eggs and young first instar thrips. These stages are most vulnerable to these predators (Nomikou et al., 2004; R. van Maanen, pers. obs.). Adult female predators (8–11 days old since egg stage) were tested individually on a leaf disc (diam. 24 mm) with one of the three different diets. The numbers of whitefly eggs ranged from 21 to 59 eggs/leaf disc and the numbers of young first instars thrips were 8 or 15/leaf disc. Previous predation tests showed that these densities are high enough to ensure maximum prey consumption (Nomikou et al., 2002). Cohorts of whitefly eggs were prepared in advance (Nomikou et al., 2003b) and first instar thrips larvae were reared on cucumber leaves with cattail pollen placed on wet cotton wool in Petri dishes. The numbers of both thrips and whiteflies in the mixed diet were equal to the single prey diets, hence, supplied additively. Predation was recorded as the number of whitefly eggs consumed (as judged by the transparent cuticle) and first-instar thrips consumed (as judged by the remains) after 24 and 48 h. Because oviposition rates are affected by the previous food source of the adult predatory mites (Sabelis, 1990), we discarded data from the second day of the experiment only (Sabelis, 1986). Oviposition was compared between days and diets using a generalized linear mixed effects model with Poisson errors and a random factor within replicates to correct for pseudoreplication, using R (lmer, R Development Core Team 2005). Predation was analysed for thrips larvae and whitefly eggs separately with generalized linear models with Poisson error distributions and diet as factor.

For the effects of diet on juvenile survival and development, we placed between 80 and 100 female mites from the culture on a plastic arena with cattail pollen. After less than 24 h, we transferred their eggs to clean cucumber leaf discs, each egg on a separate disc. We transferred the larva, directly after emerging, to a leaf disc with whitefly eggs, young first-instar thrips or a mixture of whitefly eggs and young first-instar thrips. Every other day, mites were transferred to a new leaf disc with whitefly eggs, young first-instar larvae or the two prey together. Survival and stage of the predator were recorded daily until the mites reached adulthood. Kaplan–Meier survival curves on different diets were fitted and compared using the log-rank test (Hosmer and Lemeshow 1999, library survival, R Development Core Team, 2005). Juvenile development was analysed using a time-to-event analysis with log-rank tests. Three

replicates were performed with 45, 45 and 37 individuals, the first 2 with 15 individuals per diet, the last with 8 individuals on a mixed diet, 15 on a thrips diet and 14 on a diet of whiteflies.

3. Results

3.1. Greenhouse experiments

3.1.1. Thrips

There was a clear effect of treatment on thrips densities (Fig. 1, lme: $F_{3,377} = 124.8$, $p < 0.0001$). *Amblyseius swirskii* reduced thrips to very low densities (Fig. 1A). The highest thrips densities were observed at the first assessment after 4 weeks, after which they went down to less than one larva per leaf in the following weeks (Fig. 1A). *E. ovalis* was less successful in controlling thrips; the ultimate density was between 80 and 20 larvae per leaf (Fig. 1B, difference between *A. swirskii* and *E. ovalis*: model simplification after linear mixed effects model (lme), thrips only: Log likelihood ratio (LR) = 167.1, $df = 8.7$, $p < 0.0001$, thrips plus whitefly: LR = 140.1, $df = 8.7$, $p < 0.0001$). This result is qualitatively similar to earlier experiments in which ultimate thrips densities were four times higher in the presence of *E. ovalis* than in the presence of *A. swirskii* (Messelink et al., 2006). In the treatments with the two pest species
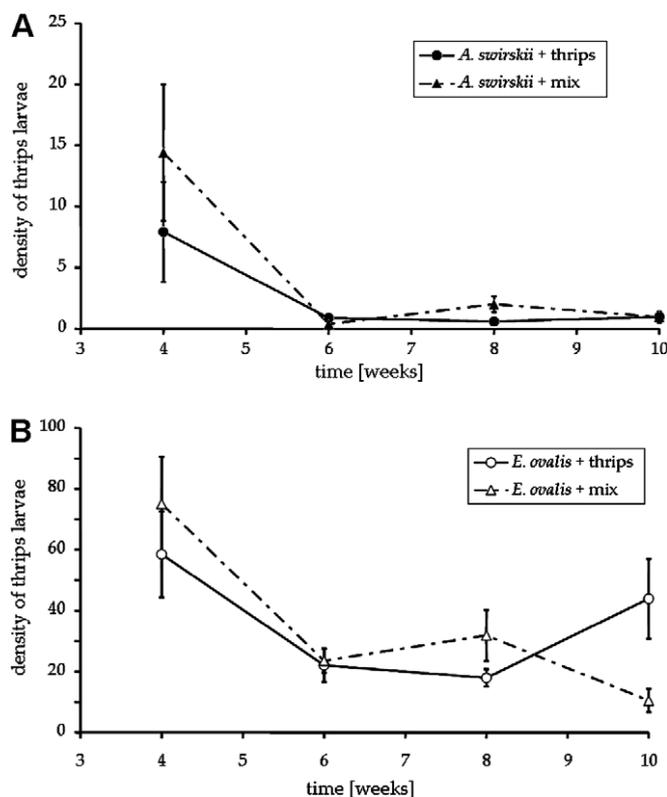

Fig. 1. The dynamics of Western flower thrips during a 10-week greenhouse experiment in presence of the predatory mites *A. swirskii* (A) and *E. ovalis* (B). Shown are average densities (±SEM) of thrips larvae in the presence (triangles) or absence (circles) of greenhouse whiteflies.

present, densities of thrips were not affected by the presence of whiteflies, irrespective of whether *A. swirskii* or *E. ovalis* was the shared predator (Fig. 1A and B, *A. swirskii*: LR = 0.019, df = 8.7, p = 0.89, *E. ovalis*: LR = 2.17, df = 6.7, p = 0.14).

3.1.2. Whiteflies

There was a significant effect of treatment on densities of whiteflies (Fig. 2, $F_{3,377} = 69.2$, $p < 0.0001$), but neither of the two predators could prevent an increase in the populations of whiteflies, resulting in thousands of immature whiteflies per leaf (Fig. 2A and B). However, the predators delayed the population increase of whiteflies considerably compared to that expected under exponential growth and to that observed in earlier experiments without predatory mites (Messelink, pers. obs.). *E. ovalis* was more successful in controlling whiteflies than *A. swirskii* when thrips were absent (Fig. 2A and B, LR = 64.1, df = 8.7, $p < 0.0001$).

In the treatments with both thrips and whiteflies, the two predators reduced densities of whiteflies clearly more than in the treatments without thrips (Fig 2A and B, *A. swirskii*: LR = 113.1, df = 8.7, $p < 0.0001$; *E. ovalis*: LR = 24.2, df = 8.7, $p < 0.0001$). *Amblyseius swirskii* reduced whitefly densities more than *E. ovalis* (Fig. 2A and B, LR = 146.0, df = 8.7, $p < 0.0001$). In the case of

A. swirskii, whiteflies went practically extinct (Fig. 2A), and with *E. ovalis*, densities of whiteflies went down from a peak of approximately 1000 immatures per leaf in the sixth week, to approximately 500 immatures per leaf in the tenth week (Fig. 1B). This suggests an indirect interaction between thrips and whiteflies mediated by the shared predator (apparent competition) or via the host plant.

3.1.3. Predators

There was a significant effect of the pest species on the densities of predators (lme: *A. swirskii*: $F_{2,282} = 151.0$, $p < 0.0001$; *E. ovalis*: $F_{2,282} = 131.1$, $p < 0.0001$). Compared to the treatments involving single pest species, the presence of thrips and whiteflies together resulted in higher densities of *A. swirskii* (Fig. 3A, thrips vs. mix: LR = 128.2, df = 7.6, $p < 0.0001$; whitefly vs. mix: LR = 189.5, df = 7.6, $p < 0.0001$), but the difference in densities between treatments with single pest species was also significant (Fig. 3A, thrips vs. whitefly: LR = 9.3, df = 7.6, $p = 0.0023$). The same was found for *E. ovalis*, (Fig. 3B, thrips vs. mix: LR = 126.3, df = 7.6, $p < 0.0001$; whitefly vs. mix: LR = 168.4, df = 7.6, $p < 0.0001$, thrips vs. whitefly: LR = 6.4, df = 7.6, $p = 0.011$). Together with the lower densities of whiteflies in the treatments with both pests, these findings are suggestive of apparent competition between thrips and whiteflies on whitefly densities.
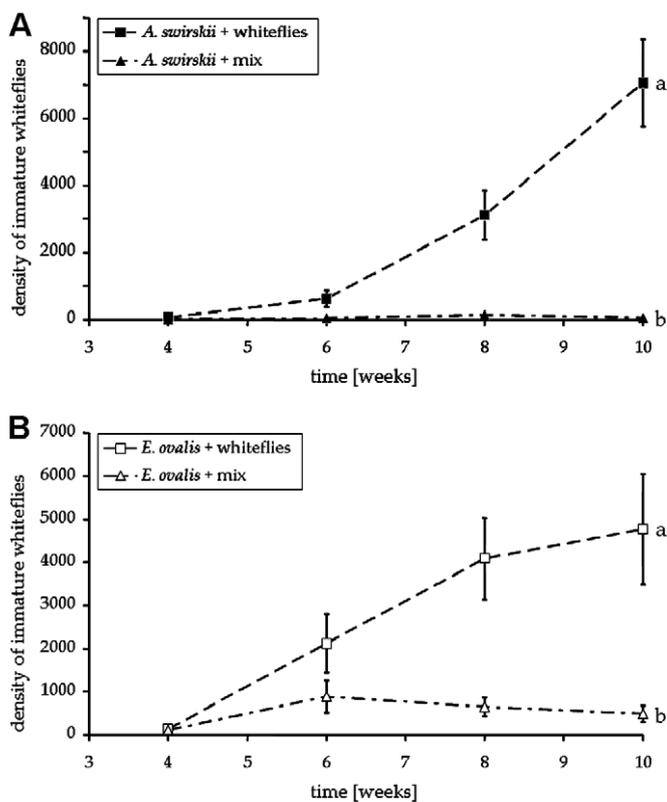

Fig. 2. The dynamics of greenhouse whitefly on cucumber plants during a 10-week greenhouse experiment in presence of the predatory mites *A. swirskii* (A) and *E. ovalis* (B). Shown are average densities (±SEM) of immature whiteflies in the presence (triangles) or absence (squares) of thrips.
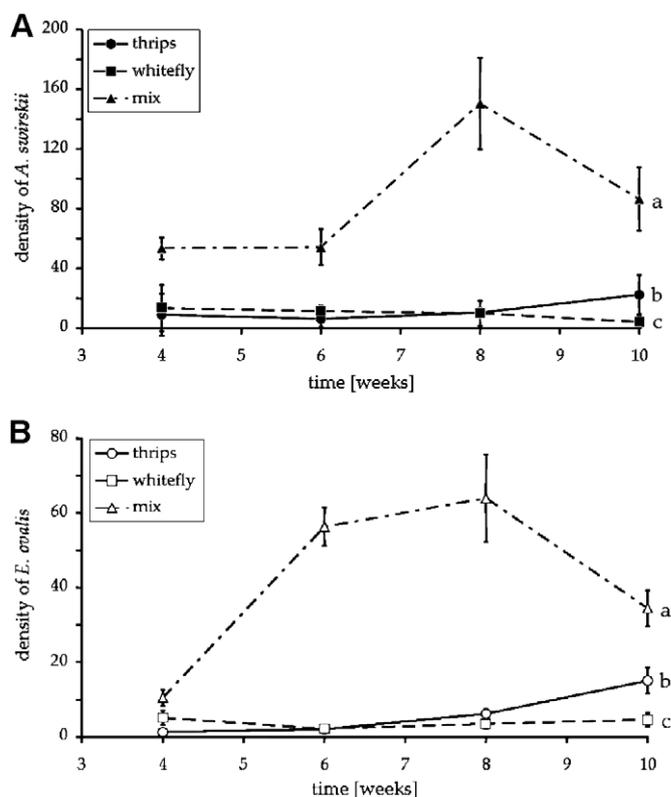

Fig. 3. The dynamics of predatory mites on cucumber plants during a 10-week greenhouse experiment. Shown are average densities (±SEM) of (A) *A. swirskii* and (B) *E. ovalis* with thrips (circles), whitefly (squares) or a combination of thrips and whiteflies (triangles).

3.2. Oviposition, juvenile survival and development and predation

The average oviposition rates of *A. swirskii* on a diet of whitefly eggs, first instar thrips or on a mixed diet were not significantly different (Fig. 4, mixed effects model). Predation, however, differed significantly with diet (Fig. 5, thrips: $F_{1,69} = 23.5$, $p < 0.0001$, whitefly: $F_{1,66} = 61.6$, $p < 0.0001$). When offered the mixed diet, *A. swirskii* consumed roughly half the numbers of each prey, as compared to experiments with single-species diets. All individuals under test consumed the two prey species. Hence, the population of predators tested did not consist of a mixture of individuals that specialized on one prey.

Juvenile survival was significantly affected by diet ($\chi^2 = 10.7$, $df = 2$, $p = 0.0047$). There was no mortality on a diet consisting of thrips or on the mixed diet, whereas

Fig. 6. Development of juveniles of the predatory mite *A. swirskii* on a diet of thrips (circles), whitefly (squares) or a combination of thrips and whiteflies (mixed diet, triangles). Shown are the cumulative proportions of juveniles that developed into adults.

some 34% of the juvenile predators that were feeding on whitefly eggs died. The rate of juvenile development (egg-to-adult) was strongly affected by diet (Fig. 6, log-rank test: $\chi^2 = 28.9$, $df = 2$, $p < 0.001$). The difference in development was significant among all three diets (Fig. 6, all p's < 0.035).
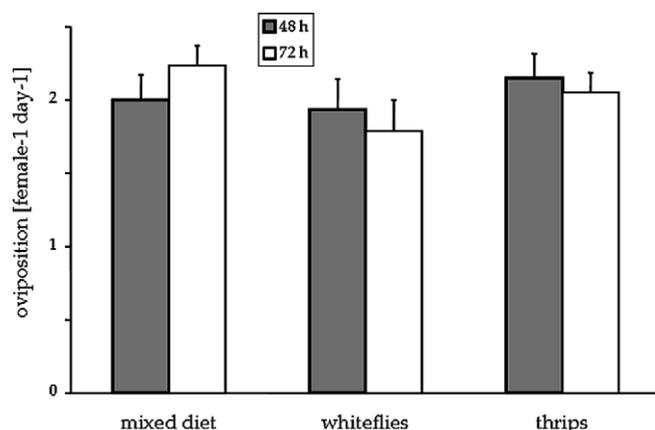
Fig. 4. Average oviposition rates of young adult females of *A. swirskii* on a diet of thrips larvae, whitefly eggs, or a combination of the two (mixed diet). Shown are average numbers of eggs (+SEM) per female per day measured after 48 and 72 h since the predators were allowed to feed on these prey.

4. Discussion

We investigated whether the use of a single species of natural enemy for biological control of two pests resulted in better control of the two pest species through an increase in predator densities (apparent competition). Alternatively, it could result in temporal escape of one of the two pest species (apparent mutualism). Our results support the first hypothesis and not the second; we found significantly higher abundance of the shared predators and lower levels of whiteflies, one of the two herbivore species. Thus, control of whiteflies was improved by the presence of thrips, but the control of thrips was not affected by the presence of whiteflies. Such asymmetric effects of prey species on each other through a shared predator have also been referred to as indirect amensalism rather than apparent competition (Chaneton and Bonsall, 2000). Perhaps the lack of an effect of the presence of whiteflies on the population densities of thrips was caused by the low initial densities of thrips. Possibly, experiments with higher initial densities of thrips would reveal a positive effect of the presence of whiteflies on the control of thrips.

We found no evidence that either of the two pest species had a positive effect on the other species in the greenhouse. In the laboratory, however, predation rates on each prey was halved in the presence of the other species. This was probably caused by satiation of the predators owing to the higher total density (whitefly plus thrips) of prey. Because the total density of prey in the greenhouse experiments was also higher in the treatments with mixed prey, there might have been similar short-term positive effects of the two prey on each other through satiation of the
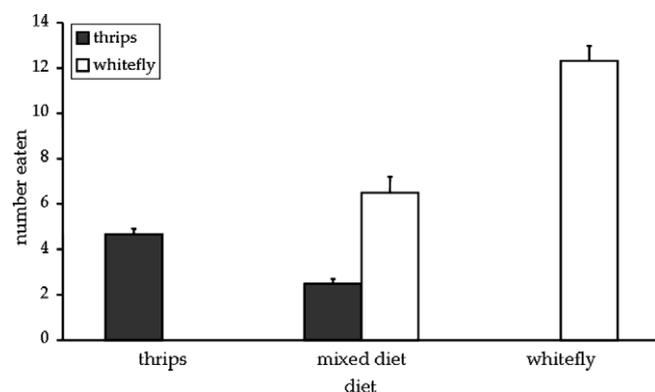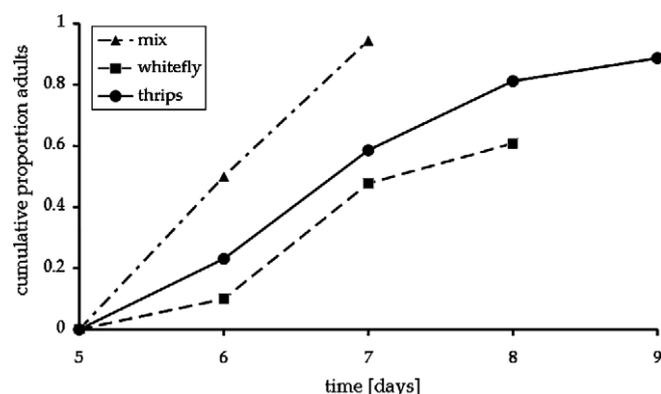
Fig. 5. Average predation rates by young adult females of *A. swirskii* on thrips larvae and whitefly eggs when offered either of these two prey species separately or in combination (mixed diet). Data are from the same experiment as shown in Fig. 4. Shown are average number of prey consumed (+SEM) per female per day measured after 48 h since the predators were allowed to feed on these prey.

predators, but they were probably not detected because they were masked by an increase in predator populations during the first four weeks. Experiments should therefore be done in which the populations of prey and predators are sampled more frequently early in the experiment.

Densities of predator species reached much higher levels in presence of both pest species; predator densities were up to 15 times higher compared to the situation with only thrips or whiteflies. This may have been partly caused by differences in the amount of food present: in the treatment with *A. swirskii* and thrips, densities of thrips were low (<1 larva/leaf). Hence, the low numbers of predators may have been a direct consequence of low numbers of prey. The density of thrips larvae in combination with *E. ovalis* was always high (>17 larvae/leaf). Thus, the low numbers of this predator cannot have been caused by low prey densities. Moreover, in the treatments with whiteflies and predators, densities of whitefly immatures were always high (>67 immatures/leaf with *A. swirskii* and >138 immatures/leaf with *E. ovalis*), suggesting that food was also not limiting in these treatments. Thus, the high numbers of predators in the treatments with both pests must have another cause besides prey densities.

To assess whether the higher predator densities were caused by differences between a mixed diet and the two single-species diets, we measured oviposition and survival in the laboratory. Oviposition on a mixed diet was not higher than on a diet of each of the two pest species alone. However, pest densities in the laboratory were never limiting for oviposition—the predators consumed at most half of the prey present—whereas densities in the greenhouse might have been. Hence, it cannot be ruled out that higher predator densities in the greenhouse were caused by increased availability of prey. In the laboratory, juvenile survival was affected by diet, and was significantly higher on a mixed diet than on either prey species separately. Likewise, developmental rate was also highest on a mixed diet. These differences in survival and developmental rate were not caused by increased availability of prey in the treatments with the mixed diet, because densities were always sufficiently high to avoid prey shortage. Hence, the higher juvenile survival and developmental rate were a result of the mixture of prey. This better juvenile performance on a mixed diet may also explain the differences in predator density observed in the greenhouse. Assuming exponential population growth of the predatory mites, the small changes in growth rate due to an increase in juvenile survival and developmental rate as observed here, would have enormous effects on numbers of predators: after 8 weeks, the predator population on the mixed diet would be seven times as high as on a single thrips diet and 27 times as high as on a single whitefly diet. We suspect that the high densities of *E. ovalis* in the mixed species treatment has a similar cause. However, it must be noted that both thrips and whiteflies were present in sufficiently high numbers in the laboratory experiment, whereas thrips levels in the greenhouse were relatively low compared to whitefly densities.

Possibly, a few thrips larvae in a diet of whiteflies already have a strong impact on population growth of the predatory mites. However, it is also possible that most first-instar thrips larvae were consumed by the predators, present in high numbers, shortly after emerging from the eggs, resulting in an underestimate of the density of thrips larvae in the greenhouse.

When comparing *A. swirskii* with *E. ovalis*, it can be concluded that *A. swirskii* is a much better predator of thrips, confirming earlier experiments on cucumber (Messelink et al., 2006), and a better predator of whiteflies when thrips is also present as prey (this experiment). These differences might even be higher in reality because of the free migration of pests between the two predator treatments.

In conclusion, our results demonstrate that increased control of pests can be achieved through apparent competition between two pest species. Whereas earlier studies focused on the use of a non-pest species to increase predator densities (Karban et al., 1994; Hanna et al., 1997; Liu et al., 2006), this study shows that similar results can be reached with two pest species that share a predator species. A further novelty of this study is the indication that the consumption of a mixed diet increases the densities of the natural enemies, not just because of a higher availability of food, but because a mixed diet results in higher growth rates of the predator populations through an increase in juvenile survival, resulting in further reduction of pest densities. We therefore suggest that the effects of mixed diets should be addressed in experimental and theoretical studies of apparent competition.

Nowadays, *A. swirskii* is increasingly used for biological control of thrips and whiteflies in many crops. Biological control strategies in these crops might be improved by tolerating acceptable levels of both thrips and whiteflies in order to stimulate population growth of predatory mites. Further research is needed to clarify relationships between pest levels and yield to enable implementation of results like these.

Acknowledgments

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