Host-plant species modifies the diet of an omnivore feeding on three trophic levels

Sara Magalhães, Arne Janssen, Marta Montserrat and Maurice W. Sabelis

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The diet choice of omnivores feeding on two adjacent trophic levels (either plants and herbivores or herbivores and predators) has been studied extensively. However, omnivores usually feed on more than two trophic levels, and this diet choice and its consequences for population dynamics have hardly been studied. We report how host-plant quality affects the diet choice of western flower thrips feeding on three trophic levels: plants (cucumber or sweet pepper), eggs of spider mites and eggs of a predatory mite that attacks spider mites. Spider mites feed on the same host plants as thrips and produce a web that hampers predator mobility. To assess the indirect effects of spider mites on predation by thrips, the thrips were offered spider-mite eggs and predatory-mite eggs on cucumber or sweet pepper leaf discs that were either clean, damaged by spider mites but without spider-mite web, or damaged and webbed. We show that, overall, thrips consumed more eggs on sweet pepper, a plant of low quality, than on cucumber, a high quality host plant. On damaged and webbed leaf discs (mimicking the natural situation), thrips killed more predator eggs than spider-mite eggs on sweet pepper, but they killed equal numbers of eggs of each species on cucumber. This is because web hampered predation on spider-mite eggs by thrips on sweet pepper, but not on cucumber, whereas it did not affect predation on predatory-mite eggs. We used the data obtained to parameterize a model of the local dynamics of this system. The model predicts that total predation by the omnivore has little effects on population dynamics, whereas differential attack of predator eggs and spider-mite eggs by the omnivore has large effects on the dynamics of both mite species on the two host plants.

S. Magalhães, A. Janssen, M. Montserrat and M. W. Sabelis, Univ. of Amsterdam, IBED, PO Box 94084, NL-1090 GB Amsterdam, the Netherlands. Present address for SM: Laboratoire Génétique et Environement, Institut des Sciences de l'Evolution, Place Eugène Bataillon, CC 065, FR-34095 Montpellier Cedex 05, France (magalhaes@isem. univ-montp2.fr).

Omnivory is a common feature of many food webs (Polis et al. 1989, Polis and Winemiller 1996, Coll and Guershon 2002). Theory predicts that omnivory may destabilize food webs (Pimm and Lawton 1978), but it may also increase the resilience of stable systems (Pimm and Lawton 1978) and the persistence of unstable systems (McCann and Hastings 1997, McCann et al. 1998), especially when foragers are adaptive (Kondoh 2003). Intraguild predation is a special case of omnivory in which a top predator feeds on its competitor and on

their shared resource (Polis and Holt 1992). Intraguild predation tends to destabilize linear food chains at intermediate and high productivity levels (Holt and Polis 1997, Mylius et al. 2001). Since intraguild predation is an interaction between two competitors, the dynamics of systems with intraguild predation can be compared to those of systems with competitors that do not kill each other. The incorporation of intraguild predation in the Lotka–Volterra competition model is expected to promote persistence due to a reduction in

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resource overlap between competitors (Holt and Polis 1997). Empirical studies have tested these predictions, for example with arthropod food webs on plants (Fagan 1997, Snyder and Ives 2001). However, the theory, and the experiments developed to test it, mainly concern omnivores feeding on two adjacent trophic levels, whereas many omnivores feed on three or even more trophic levels (Polis et al. 1989, Fagan 1997, Armer et al. 1998, Eubanks and Denno 2000).

Plant-feeding omnivores consume more herbivores on host plants of low quality than on high quality plants (Agrawal et al. 1999, Agrawal and Klein 2000). Hence, herbivores are expected to be less abundant on low-quality plants than on high-quality plants, both because of the direct effect of host-plant quality on the growth rates of herbivores and because of the indirect effect of host-plant quality on the diet choice of omnivores. However, omnivores may also feed on the natural enemies of the herbivores, and this consumption is also affected by host-plant quality (Janssen et al. 2003). Hence, the effect of omnivores on the population dynamics of their herbivorous prey hinges on the differential effect of plant quality on the omnivore consumption of plant tissue, herbivores and natural enemies of the herbivores (Venzon et al. 2001). In this article, we study the effect of host-plant quality on the diet choice of a plant–inhabiting omnivorous thrips feeding on a linear, tritrophic system involving predatory mites, herbivorous spider mites and plants (Fig. 1).

Western flower thrips (*Frankliniella occidentalis*, Pergande) feed on several host plants, including cucumber and sweet pepper (Lewis 1973). In addition, they kill the eggs of *Tetranychus urticae* (Koch), a herbivorous spider mite (Trichilo and Leigh 1986) and the eggs of *Phytoseiulus persimilis* (Athias-Henriot), a predatory mite specialised on spider mites (Janssen et al. 2003). Previous studies have shown that the developmental rate and the juvenile survival of thrips are lower on sweet pepper than on cucumber (Janssen et al. 2003). Hence, for thrips, cucumber is a host plant of better quality than sweet-pepper. Moreover, thrips consume more eggs of spider mites (Agrawal et al. 1999, Agrawal and Klein 2000) and of *P. persimilis* (Roda et al. 2000, Janssen et al. 2003) on low-quality host plants than on host plants of high quality. However, this predation of mite eggs by thrips was assessed for each mite species separately (Trichilo and Leigh 1986, Wilson et al. 1996, Agrawal et al. 1999, Agrawal and Klein 2000, Roda et al. 2000, Janssen et al. 2003), whereas the effect of omnivory on population dynamics in this system can only be investigated when both mite species are present at the same time.

We studied diet choice of western flower thrips on cucumber and sweet-pepper plants in presence of spider mites and predatory mites. In addition, we assessed the indirect effects of herbivores on the predation rate of omnivores. First, the damage produced by spider mites on
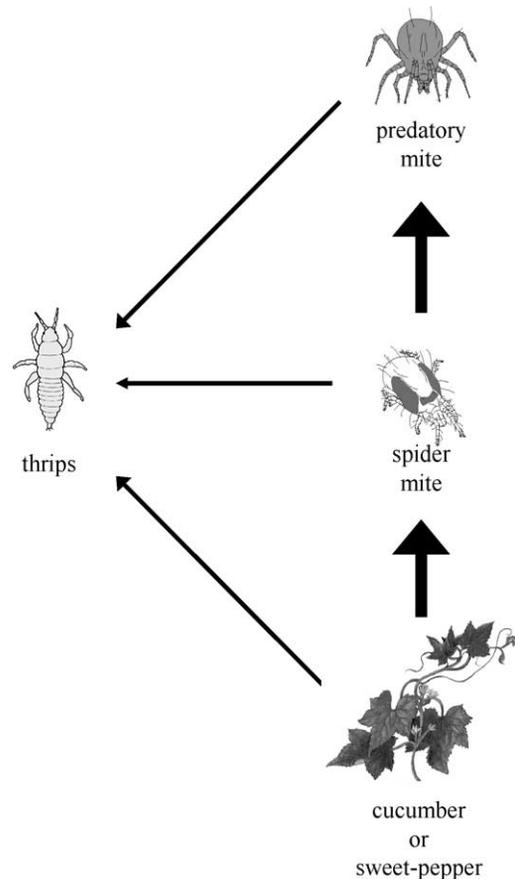

Fig. 1. Schematic representation of the system under study.

plant tissue may affect host-plant quality and thereby the predation rate of thrips (Agrawal and Klein 2000). Second, spider mites produce webs, the structure of which differs among plants (Gerson 1985). This web confers protection of eggs against predators (Sabelis 1981, Gerson 1985, Sabelis and Bakker 1992), including thrips (Trichilo and Leigh 1986, Roda et al. 2000). Hence, variation in web structure among plants may differentially affect the predation rates of omnivores on different plants. We investigated the consequences of our findings for the population dynamics of these species, using a model that predicts the dynamics of spider-mite and predatory-mite populations in absence of omnivory (Diekmann et al. 1988, Janssen and Sabelis 1992, van Baalen and Sabelis 1995, Pels and Sabelis 1999). In the model analysis, we explore the effects of the relative and the total predation rate of the omnivore on population dynamics.

Material and methods

All species were cultured as described in Janssen et al. (1999). Experiments were performed in a climate room

(25°C, 70% RH and 16h light). Cohorts of first instar (L1) thrips larvae were obtained from females ovipositing on cucumber leaves with pollen (*Typha* spp.) during 24 h. These leaves were placed on wet cotton wool in a plastic petri dish (∅ 14 cm) closed with a lid, the centre of which had a hole (∅ ±7 cm) covered with gauze, to allow for ventilation and prevent escapes.

Predation rates

Leaf discs (∅ 15 mm) were cut from cucumber or sweet pepper leaves, placed dorsal side down on wet cotton wool in a 100-ml plastic vial (∅ 5 cm), then they were allocated to three different treatments: (1) "undamaged" leaf discs, with eggs of predatory mites and of spider mites (1-day old, to minimize hatching during the experiment) added manually to the disc; (2) "damaged" leaf discs, which received 20 spider-mite females during the 2 days that preceded the experiment (to cause damage, produce web and eggs), and 10 predatory-mite females, introduced 12 h before the experiment (to kill spider-mite eggs and lay eggs of their own), then all adult prey and predator were removed before the experiment; (3) leaf discs "damaged without web", infested as in (2) but with web, adults and eggs removed with a brush and eggs of both species added manually thereafter. In all three treatments, the number of eggs per species varied among leaf discs (from 12 to 25), but each leaf disc had equal numbers of eggs of each species (eggs in excess were removed with a fine needle). Replicates where mite larvae had emerged from the eggs during the experiment were discarded.

First instar thrips larvae were placed either on cucumber or on sweet-pepper leaves during 24 h, where they developed into the second instar. Subsequently, thrips larvae were placed individually on leaf discs from the same host species on which they had been feeding the previous day. These leaf discs had received one of the treatments described above. One day later, the mite eggs killed by thrips were counted. Other causes of egg mortality were negligible. Due to escape of some thrips larvae, sample sizes were not equal, but ranged from 29 to 36 (Fig. 2).

Behavioural observations

To measure searching time and encounter rates, we recorded the behaviour of thrips larvae on some of the "damaged" leaf discs during the first hour of the predation experiment (cucumber: N = 15; sweet pepper: N = 16). We chose to study the behaviour on "damaged" discs because thrips will encounter mite eggs on damaged and webbed leaves under natural conditions. Searching time was defined as the time that thrips larvae spent walking and encounter rates as the frequency with
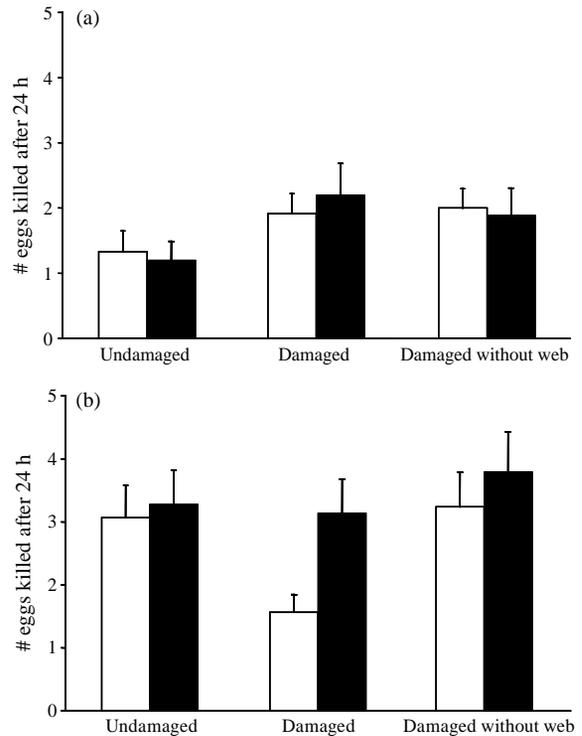

Fig. 2. Predation of eggs of spider mites (white bars) and of eggs of predatory mites (black bars) by second instar thrips larvae on leaf discs of (a) cucumber and (b) sweet pepper. Vertical lines correspond to standard errors of the mean. First two bars: undamaged leaf discs, middle bars: damaged leaf discs with spider-mite web, two last bars: damaged leaf discs without web. Sample sizes for cucumber were 30, 35 and 36 and for sweet pepper 29, 30, 29 for undamaged, damaged and damaged leaf discs without web, respectively.

which they touched eggs of one species with their antennae per unit searching time. We calculated the success ratio as the number of eggs of one mite species killed relative to the number encountered. Replicates in which no encounters with eggs of one species occurred were excluded from the calculation of the success ratio for the eggs of that species. Because predation events were rare during the hour of observation, we measured handling time in a separate experiment, in which we placed 15 eggs of each species on clean cucumber leaf discs (N = 14) or on sweet-pepper discs (N = 10) together with three thrips larvae, then recorded thrips behaviour during 24 h, using a camera mounted on the stereoscope and connected to a time-lapse video recorder. Handling time was defined as the time that elapsed since thrips larvae grabbed the egg with their front legs until they removed their mouthparts from the egg remains. While analyzing the recordings, we observed that some eggs were only punctured (i.e. thrips larvae inserted their mouthparts into the egg and pierced it, but immediately moved on without having fed). We present the fraction of eggs punctured in each replicate relative to the total

number of eggs killed, but do not include punctured eggs in our calculations of handling time. Since we did not control for the age of the eggs in these observations, some of them hatched during the test period (on average 0.79 ± 0.318 on cucumber and 1.00 ± 0.365 on sweet pepper). On sweet pepper, some thrips larvae ate larvae of predatory mites. The handling time for this prey type is presented separately.

Statistical analysis

Predation rates were log-transformed to obtain normality and compared between plant species and among treatments (undamaged, damaged and damaged without web) using a two-way MANOVA, with plant species and treatment as main effects, and predation on eggs of predatory mites and eggs of spider mites as the dependent variables. The initial number of eggs per species was introduced as a covariable, but it was not significant and thus removed from further analysis. Subsequently, we performed planned comparisons between predation on the two host plants within the same treatment. Significance levels were corrected with the sequential Bonferroni method for multiple comparisons (Sokal and Rohlf 1995). Within each treatment, we applied a paired t-test to assess whether thrips larvae preyed more on eggs of one of the two species. This was done for the treatment with damaged and webbed discs and for the treatment where discs were damaged and without web. To specifically test the effect of the web on predation rates on eggs of spider mites and of predatory mites, predation rates on eggs of each species on webbed and unwebbed damaged discs were compared using a two-sample t-test.

In the behavioural observations, differences in searching time on the two plant species were analyzed using a t-test. The Mann–Whitney U-test was used to compare encounter rates with eggs of each species, the success ratio and the fraction of eggs punctured between plant species (Field 2000). On each host plant, differences in encounter rates with eggs of each species and in the fraction of eggs punctured were compared using Wilcoxon signed rank tests. This statistical test was not applied to the success ratio because of too few observations (five replicates on cucumber and three on sweet pepper yielded values of success ratios for both species). Differences in handling times (between egg species on each host plant and of each egg species between host plants) were analyzed by calculating the harmonic mean of handling time per replicate, then performing the same tests as above. We did not include the handling time of *P. persimilis* larvae in the analysis because predation of thrips on this prey type occurred rarely.

Model

We incorporated omnivory in a predator–prey model that yields good predictions for the population dynamics of this system in absence of omnivory (Diekmann et al. 1988, Janssen and Sabelis 1992, van Baalen and Sabelis 1995, Pels and Sabelis 1999) to analyze how total and relative predation by omnivores on spider mites and predatory mites affects population dynamics. Subsequently, we used the predation rates of the omnivorous thrips as measured in our experiments to predict what type of dynamics are expected on cucumber and sweet pepper. See Appendix 1 for further details.

Results

Predation rates

There was a significant effect of host plant on the number of mite eggs killed (Table 1). Thrips larvae killed significantly more eggs of spider mites and of predatory mites on sweet pepper, a host plant of low quality than on cucumber, a high-quality host plant (Fig. 2). The difference in predation rates on the two host plant species was significant on undamaged discs (planned comparisons with Bonferroni correction, $p = 0.001$), and on damaged discs without web ($p = 0.018$), but only marginally significant on damaged discs with web ($p = 0.07$). This last treatment mimics the natural situation: plants containing spider mites always contain web and damage.

The relative predation rate of thrips larvae on eggs of the two mite species also varied with host plant and with treatment. On cucumber, thrips larvae killed equal numbers of eggs of the two species on all treatments (Fig. 2a; paired t-test, clean: $T_{29} = 0.453$, $p = 0.654$; damaged: $T_{34} = -0.131$, $p = 0.896$; damaged without web: $T_{35} = -1.41$, $p = 0.17$). On clean sweet pepper discs and on sweet pepper discs that were damaged but without web, thrips larvae killed equal numbers of eggs of the two species (Fig. 2b, first two bars, $T_{29} = 20.453$, $p = 0.65$ and last two bars, $T_{28} = 1.102$, $p = 0.28$) but they killed more eggs of predatory mites than of spider mites on damaged and webbed sweet pepper leaf discs (Fig. 2b, middle bars, $T_{29} = 2.764$, $p = 0.01$). Thrips killed significantly more eggs of spider mites on damaged sweet pepper leaf discs without web than on leaf discs with web

Table 1. Results of a two-way MANOVA on the log-transformed number of spider-mite eggs and predatory-mite eggs killed. The degrees of freedom indicated are of the model and the error, respectively.

Factor	Wilks' lambda	F (df)	P
Host plant	0.893	10.89 (2, 182)	0.000034
Treatment	0.969	1.46 (4, 364)	0.213
Interaction	0.968	1.49 (4, 364)	0.216

(compare white bars of the second and the third set of bars of Fig. 2b, $T_{57} = 5.454$, p = 0.023), while predation on predatory-mite eggs did not differ (compare black bars of the second and the third set of bars, $T_{57} = 0.482$, p = 0.49). Hence, web on sweet pepper hampered predation by thrips on spider-mite eggs, but not on predatory-mite eggs. This effect was not observed on cucumber. Therefore, web affected the relative predation rate of thrips on eggs of spider mites and of predatory mites on sweet pepper, but not on cucumber.

To assess whether the damage caused by spider mites on leaf tissue affected predation by thrips, we compared predation on undamaged leaf discs to predation on damaged leaf discs without web, thereby excluding the effect of web on predation. Thrips killed at least 50% more eggs of both mite species on infested cucumber than on clean cucumber (Fig. 2a, compare first and third pairs of bars), but such a trend was not observed on sweet pepper (Fig. 2b). However, differences were not significant on any of the two host plant (cucumber: MANOVA, Wilks' $\lambda_{2,63} = 1.924$, p = 0.154, sweet pepper: MANOVA, Wilks' $\lambda_{2,55} = 0.053$, p = 0.948, Fig. 2).

In summary, host-plant quality affected the total predation rate of thrips on eggs of the two species, resulting in a higher predation rate of the omnivore on eggs of the two mite species on the low-quality sweet pepper than on the high-quality cucumber. In addition, spider-mite web affected the relative predation rate on eggs of spider mites versus eggs of predatory mites on sweet pepper, but not on cucumber. On the treatment mimicking the natural situation (damaged leaf discs with web), the combined effect of these factors resulted in a difference in the relative predation rate of thrips between host plants, but in a small difference in the total predation rate.

Behavioural observations

On damaged and webbed leaf discs, the searching time and encounter rates with eggs of each species did not differ significantly between host plants (Table 2; searching time: t-test, $T_{29} = 1.229$, p = 0.275; encounter rates: Mann–Whitney U-test, U = -0.56, p = 0.626 for spider-mite eggs and U = -0.53, p = 0.626 for predatory-mite eggs). On cucumber, the encounter rates with eggs of the two species were not significantly different (Table 2; Wilcoxon signed rank test, Z = -0.46, p = 0.624), but thrips larvae tended to encounter more predatory–mite eggs than spider-mite eggs on sweet pepper, although this difference only bordered significance (Table 2; Wilcoxon signed rank test, Z = -1.9, p = 0.055). The success ratio for eggs of spider mites did not differ significantly from that of predatory-mite eggs on each of the two host plants (Table 2; Mann–Whitney

U-test, cucumber: U = -1.11, p = 0.397, sweet pepper: U = -0.26, p = 0.887).

Handling times of eggs by thrips larvae were not affected by host plant species (Table 2; spider-mite eggs: Mann–Whitney U-test, U = -1.63, p = 0.113; predatory-mite eggs: U = -1.414, p = 0.188). The handling time of spider-mite eggs did not differ significantly from that of predatory-mite eggs (cucumber: Wilcoxon signed rank test, Z = -1.83, p = 0.068; sweet-pepper: Wilcoxon signed rank test, Z = -0.56, p = 0.575). Thrips larvae punctured fewer spider-mite eggs than eggs of predatory mites on each of the two host plants (Table 2; Wilcoxon signed rank test, Z = 2.53, p = 0.011 and Z = 2.8, p = 0.005 on cucumber and on sweet pepper, respectively). The number of spider-mite eggs punctured did not differ significantly between host plants (Table 2; Mann–Whitney U-test, U = -0.64, p = 0.6), but thrips punctured significantly more predatory-mite eggs on cucumber than on sweet pepper (Table 2; Mann–Whitney U-test, U = -2.64, p = 0.006). Thus, on sweet pepper, the low quality plant, thrips larvae killed more eggs of predatory mites to eat them than on cucumber, the high quality plant.

Model

When thrips feed equally on eggs of the two species (relative predation rate $\eta = 0.5$), the model predicts that predation by thrips affects the total number of mites on a plant but not the time to eradication of the spider-mite populations (Fig. A1). However, a slightly higher predation rate on eggs of predatory mites results in much higher cumulative numbers of spider mites and in an increase in the time to prey eradication (Fig. A2). Predation of mite eggs by thrips larvae strongly affects the population dynamics on sweet pepper: in presence of the omnivorous thrips, the interaction time increases by 25%, resulting in a seven-fold increase in the peak density of spider mites (Fig. A3). On cucumber, predation by thrips has negligible effects on population dynamics (Fig. A3). See Appendix 1 for further details.

Discussion

The host-plant species used in this study affected the predation of omnivorous thrips larvae on mite eggs: thrips consumed more spider-mite eggs and predatory-mite eggs on cucumber, a high-quality host plant, than on sweet pepper, a host plant of low quality. Moreover, the web produced by spider mites affected predation by thrips on spider-mite eggs on cucumber, but not on sweet pepper. This web had no effect on thrips predation on predatory-mite eggs on the two host plants. Together, these effects led to a difference in the relative predation

Table 2. Foraging traits (mean±se) of thrips larvae on cucumber and sweet-pepper leaf discs with eggs of spider mites and predatory mites.

Host plant	Cucumber		Sweet pepper	
Egg species	spider mite	predatory mite	spider mite	predatory mite
Searching time[1]	12′03″±2′03″		15′17″±2′50″	
Encounter rate[2]	5.24±1.93	8.18±3.9	3.12±1.22	8.43±2.55
Success ratio[3]	0.15±0.08	0.07±0.06	0.07±0.07	0.05±0.05
Handling time[4]	16′27″± 5′29″	5′57″±2′58″	9′13″±2′54″	7′41″±2′25″
% punctured[5]	0.07±0.06	0.75±0.1	0.07±0.04	0.39±0.06

[1]time spent walking per hour (in min); [2]number of encounters per unit search time; [3]number of eggs killed per number of eggs encountered; [4]averages of handling times, calculated as harmonic means; [5]fraction of the total number of eggs attacked per replicate that were killed but not fed upon.

rate of thrips on eggs of the two mite species between host plants on damaged and webbed discs, which mimick the natural situation. On those discs, the total predation rate differed between host plants, but not significantly. Model simulations predicted that the population dynamics of spider mites and of predatory mites were strongly affected by the relative predation rate of thrips on eggs of the two species. Variation of the total predation rate of thrips on eggs of the two species was predicted to have a smaller effect on population dynamics. As a consequence, the effects of omnivorous thrips on the dynamics of a system consisting of spider mites and predatory mites are expected to be stronger on sweet pepper than on cucumber.

The effect of host-plant species

Plant-feeding omnivores are known to consume more prey on host-plants of low quality than on high-quality host plants (Coll and Izraylevich 1997, Agrawal et al. 1999, Eubanks and Denno 2000, Janssen et al. 2003). The plants used in this study differ in quality (Janssen et al. 2003) and thrips indeed consume more mite eggs on the low-quality sweet pepper than on the high-quality cucumber. Besides differing in quality, plants also vary in other aspects, such as leaf structure, and such differences may affect the foraging behaviour of plant-inhabiting arthropods. For example, trichomes are known to reduce predation of mite eggs by thrips (Roda et al. 2000). Cucumber, the plant of high quality used in our experiments, has more trichomes than sweet pepper, and differences in predation rate could also result from a different leaf topography. However, if trichomes would have caused differences in predation rates by impeding searching behaviour of the thrips larvae, we would expect differences in encounter rates with eggs of the two species on the two host plants. Since this was not found, we conclude that differences in consumption rates on the two host plant species are not due to trichomes or other structures on the leaves. We suggest that thrips consumed more mite eggs on sweet pepper to compensate for nutrient deficiencies arising from low host-plant quality. On sweet pepper, the proportion of eggs killed that were consumed was higher than on cucumber, which is in line with this possibility.

The indirect effect of the herbivore on the omnivore

Under natural conditions, thrips encounter mite eggs on leaves that are damaged by spider mites and covered with web. Under such conditions, thrips killed similar numbers of spider-mite eggs on the two host plants. This suggests that host-plant quality did not affect thrips predation on spider-mite eggs, which would contrast with previous findings (Agrawal et al. 1999). However, our experimental set-up differs from that of Agrawal et al. (1999) because we incorporate the web produced by spider mites and its possible effects on the predation by thrips. Spider-mite web did not affect predation of predatory-mite eggs by thrips and hampered predation of spider-mite eggs on sweet pepper and not on cucumber. The structure of spider-mite web varies with leaf structure and tends to be denser on tough, glabrous leaves (Gerson 1985) such as those of sweet pepper plants. On cucumber, spider-mite females suspend their web from trichomes, resulting in a relatively-open three-dimensional web structure in which thrips can move freely. In contrast, web on sweet pepper leaves is flat and dense and thrips may have problems entering it, resulting in lower predation of spider-mite eggs inside the web. Because predatory mites mainly oviposited on top of the web on sweet-pepper leaf discs (S. Magalhães, pers. obs.), there is no effect of web on predation of these eggs. The behavioural observations confirmed that thrips encountered more predatory-mite eggs than spider-mite eggs on sweet pepper, and this difference reflects that of predation rates. This suggests that differences in predation rates do not result from an inherent preference of thrips for predatory-mite eggs, but from differences in accessibility between egg species, probably related to these effects of the web structure. Thus, the differences in webs on predation by thrips on mite eggs depends on the interaction between web and leaf surface, and on the oviposition behaviour of each mite species.

Implications for population dynamics

Sweet pepper is a host plant of lower quality than cucumber. Moreover, on sweet-pepper plants, spider-mite eggs, which can serve as diet supplement, are more difficult to reach than on cucumber due to the structure of the web. Thus, thrips populations on damaged and webbed sweet-pepper plants with spider mites will probably grow slower than on cucumber plants.

Since thrips predation on spider-mite eggs does not differ much between host plants that are damaged and webbed, thrips are expected to affect the population dynamics of herbivorous mites similarly on the two host plants in absence of predators. However, the omnivorous thrips can also affect the population dynamics of herbivores by attacking the predators of these herbivores. In the system studied here, the interaction between predatory mites and spider mites is typically unstable and may result either in prey eradication or in over-exploitation of the plant (Sabelis and van der Meer 1986, Janssen et al. 1997, Pels and Sabelis 1999). On damaged and webbed sweet pepper and cucumber, the rates of total predation on mite eggs are quite similar (Fig. 2a, 2b, sum of both middle bars per plant species). However, the diet of the thrips on sweet pepper consists for a much larger part of eggs of the predatory mites than on cucumber, and this can have a large effect on the population dynamics of the mites: even when spider mites are eventually eradicated, the time it takes to eradication is strongly affected by the thrips diet (Appendix 1). We predict that such differences in omnivore diet lead to large differences in plant damage and can therefore affect plant fitness.

In this analysis, we have ignored the direct damage of the omnivore on the plant. Probably, thrips will tend to feed more on cucumber than on sweet pepper, since cucumber is a host plant of better quality. However, we expect the effect on population dynamics of thrips feeding on plants to be small compared to the effect of spider mites, since the population growth rate of thrips are much lower than that of spider mites (Sabelis 1985, van Rijn et al. 1995). Hence, we predict large differences in local dynamics of predators and prey as a result of the interaction of omnivory, host-plant quality and other host-plant effects.

Our results lead to the prediction that the effects of omnivory on population dynamics of tritrophic systems do not only depend on plant quality and on the interaction of omnivores with herbivores, but also on the interaction of omnivores with predators. We conclude that the effects of diet choice of omnivores on population dynamics should be analyzed within the context of the entire food web associated with the plant.

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Appendix 1

The local dynamics of spider mites and predatory mites can be described adequately with a simple model (Diekmann et al. 1988, Janssen and Sabelis 1992, van Baalen and Sabelis 1995, Pels and Sabelis 1999). The dynamical properties of this model are qualitatively similar to simulation models containing detailed biological information such as age structure (Sabelis and van der Meer 1986). The model is based on the assumptions that (1) the predation rate is within the plateau phase of the functional response i.e. it is constant; (2) prey populations grow exponentially in absence of predators; (3) predator populations grow exponentially in presence of prey; (4) age structure is not relevant to population dynamics; (5) predators do not disperse until prey are eradicated; (6) climatic conditions are constant. These assumptions are quite realistic for the system studied here (Sabelis and van der Meer 1986, Janssen and Sabelis 1992, Pels and Sabelis 1999).

To show the effect of the diet of an omnivore on the dynamics of the two mite species, we include predation by thrips in the model. We neglect the dynamics of the thrips because they have a slower population growth rate than both predator and prey mite species (Sabelis 1985, van Rijn et al. 1995). Predation by thrips can then be modelled by adding an extra mortality term to the equations of both mites.

If $x =$ the number of prey (spider mites), $y =$ the number of predatory mites (the specialist predator), $\alpha =$ the rate of prey population growth, $\beta =$ maximum rate of predation by the specialist predator and $\gamma =$ the growth rate of the specialist predator population, the local dynamics can be described as:

$$\frac{dx}{dt} = \alpha x - \beta y - \mu\eta \frac{x}{\eta x + (1 - \eta)y}$$

$$\frac{dy}{dt} = \gamma y - \mu(1 - \eta)\frac{y}{\eta x + (1 - \eta)y}$$

The parameter μ is a measure for total predation by the population of thrips on eggs of spider mites and of predatory mites. We assume that μ is independent of prey density (i.e. the functional response is in the plateau phase). The parameter η is a measure for the relative feeding rate of thrips on eggs of spider mites or of predatory mites (Post et al. 2000). The actual number of eggs of each species eaten depends not only on this relative predation rate, but also on the relative numbers of eggs of both species present, as expressed in the last term of both differential equations. A relative predation rate (η) of 0.5 results in eggs of both mite species being eaten in the same ratio as in which they are present, a higher η in a relative overrepresentation of spider-mite eggs in the diet relative to their presence, while a lower η results in overrepresentation of eggs of the predatory mite (Venzon et al. 2001).

The values for the growth rates of predators and prey and for the predation rate of the specialist predator are taken from Venzon et al. (2001) and given in the figure legends. The initial number of spider mites was set at 100 and that of predatory mites at 1. The model is sensitive to initial conditions only when the prey–predator ratio exceeds 20; the prey population then escapes control by

the specialist predator. With lower predator–prey ratios, the prey population will either increase at first and subsequently be eradicated, or will be eradicated without initial increase. The model has a positive equilibrium for both prey and specialist predators, but this equilibrium is unstable (M. Egas, pers. comm.).

The effect of omnivory on the population dynamics of the mites has two components. First, when omnivore feeds equally on the two mite species ($\eta = 0.5$), the maximum number of prey decreases with higher predation (i.e. more omnivores present). When spider mites are eradicated by the predatory mites, the time to extinction is unaffected by omnivory (Fig. A1). This is because eradication time is not determined by the total number of prey and predators but by the predator–prey ratio (Janssen and Sabelis 1992), which is unaffected by omnivory when $\eta = 0.5$. The time to eradication of spider mites and predatory mites is affected, however, when predation by the omnivore is high (cf. curve where $\mu = 23.5$ in Fig. A1).

The second component of omnivory that affects the mite dynamics is the relative predation rate of the omnivore on each of the two mite species. When thrips kill more spider-mite eggs, the maximum number of spider mites as well as the time to eradication of spider mites decreases (Fig. A2). The opposite trend is seen when thrips kill relatively more eggs of the predator. Indeed, increasing the relative predation rate on of thrips on predators leads to a dramatic increase in the maximum number of spider mites, due to a decrease in the growth of predator populations (Fig. A2, note differences in scale among figures). However, predators are not always eradicated (Fig. A2). From the second differential equation, it follows that a positive growth of the predator population occurs when
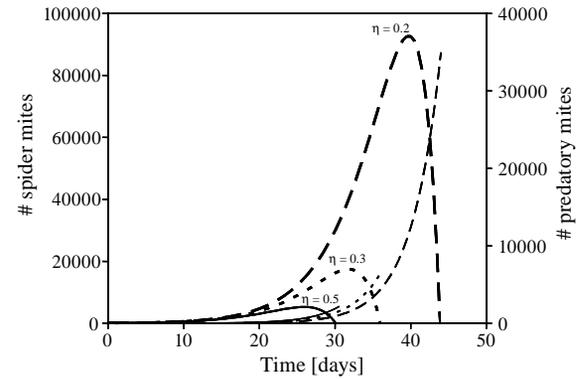

Fig. A2. Population dynamics of populations of prey (spider mites thick curves) and of predatory mites (thin curves) in absence of thrips (black drawn curve) and in presence of thrips with different relative predation rates for spider-mite eggs or eggs of predatory mites (η) (broken curves). Predation rate of mite eggs by thrips: $\mu = 4.7$ prey/day. Other parameter values are as in Fig. A1.

$$\gamma > \frac{\mu(1 - \eta)}{\eta x + (1 - \eta)y}$$

Because the omnivore kills more predatory mites than spider mites, the population of spider mites increases, resulting in the right-hand side of the above inequality to become smaller until this inequality holds and the predator population increases. Hence, as long as omnivores feed on prey as well ($\eta > 0$), a small population of predators in a large population of prey is difficult to eradicate because the omnivore encounters and attacks many more spider mites than predators.

We used the values of predation rates obtained in our experiments (Fig. 2) to compare the effects of predation by thrips on population dynamics on the two host plants
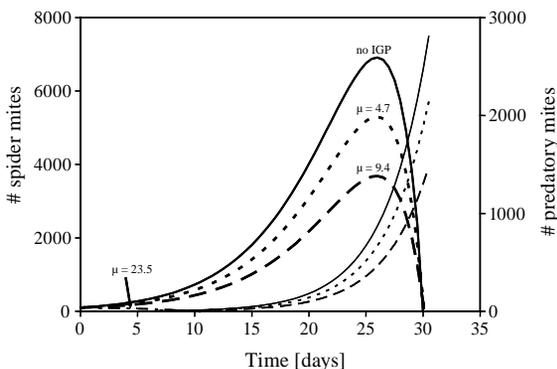

Fig. A1. Population dynamics of prey (spider mites, thick curves) and of predatory mites (thin curves) populations in absence of the ominovorous thrips (black drawn curve) and in presence of thrips with different total predation rates (μ), with equal predation rate on eggs of either species ($\eta = 0.5$) (broken curves). Other parameter values are $\alpha = 0.223$, $\beta = 1.788$ and $\gamma = 0.260$.
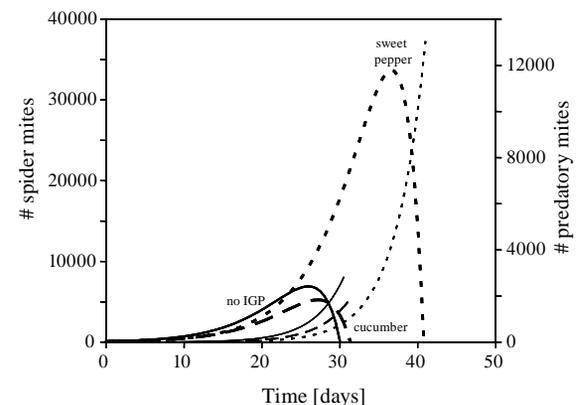

Fig. A3. Population dynamics of prey (spider mites, thick curves) and of predatory mites (thin curves) in absence of thrips (black drawn curve) and in presence of thrips on cucumber (dashed curves) and on sweet pepper (dotted curves). Absolute and relative predation rates by thrips on eggs of each of the two species are as measured on the two host plants, other parameter values are as in Fig. A1.

(Fig. A3). When combining the predation rate of thrips on spider mites relative to that on predatory mites and the total predation rate of thrips on the two species we predict that the time to prey eradication on cucumber is slightly longer in presence of omnivory, but the maximum number of spider mites is smaller. On sweet pepper, both the time to prey eradication and the maximum number of prey is larger than on cucumber or without omnivory. Hence, small differences in total and relative predation rate can result in large effects on the dynamics of herbivorous mites and their predators.