Population dynamics of thrips prey and their mite predators in a refuge

**Sara Magalhães · Paul C. J. van Rijn ·
Marta Montserrat · Angelo Pallini · Maurice W. Sabelis**

Abstract Prey refuges are expected to affect population dynamics, but direct experimental tests of this hypothesis are scarce. Larvae of western flower thrips *Frankliniella occidentalis* use the web produced by spider mites as a refuge from predation by the predatory mite *Neoseiulus cucumeris*. Thrips incur a cost of using the refuge through reduced food quality within the web due to spider mite herbivory, resulting in a reduction of thrips developmental rate. These individual costs and benefits of refuge use were incorporated in a stage-structured predator–prey model developed for this system. The model predicted higher thrips numbers in presence than in absence of the refuge during the initial phase. A greenhouse experiment was carried out to test this prediction: the dynamics of thrips and their predators was followed on plants damaged by spider mites, either with or without web. Thrips densities in presence of predators were higher on plants with web than on unwebbed plants after 3 weeks. Experimental data fitted model predictions, indicating that individual-level measurements of refuge costs and benefits can be extrapolated to the level of interacting populations. Model-derived calculations of thrips population growth rate enable the estimation of the minimum predator density at which thrips benefit from using the web as a refuge. The model also predicted a minor effect of the refuge on the prey density at equilibrium, indicating that the effect of refuges on population dynamics hinges on the temporal scale considered.

Keywords Antipredator behaviour · Population dynamics · Web · Stage-structured model · Phytoseiid mites · Thrips

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Sara Magalhães and Paul C. J. van Rijn have contributed equally to this work.

S. Magalhães (✉) · M. Montserrat · M. W. Sabelis
IBED, Institute for Biodiversity and Ecosystem Dynamics,
University of Amsterdam, Section Population Biology,
P.O. Box 94084, 1090 GB Amsterdam, The Netherlands
e-mail: magalhaes@isem.univ-montp2.fr

P. C. J. van Rijn
Netherlands Institute of Ecology (NIOO-KNAW),
Centre for Terrestrial Ecology, Heteren, The Netherlands

A. Pallini
Department of Animal Biology, Section Entomology,
Federal University of Viçosa, Viçosa, Minas Gerais, Brazil

Present Address:
S. Magalhães
Laboratoire Génétique et Environement, Institut des
Sciences de l'Evolution, Place Eugène Bataillon,
cc 065, 34095 Montpellier, France

Introduction

Prey may avoid being killed by predators either by defending themselves or by escaping. One way to escape is to move into a refuge where predation risk is reduced (Caley and StJohn 1996; Pallini et al. 1998; Martin and Lopez 1999; Holbrook and Schmitt 2002; Magalhães et al. 2002; Persson and de Roos 2003; Meyer and Byers 2005). Prey usually pay a cost of using such refuges (Lima 1998). For example, abiotic conditions may be less optimal inside than outside refuges (Polo et al. 2005), mating opportunities may be reduced (Martin et al. 2003a), or food may be of lower

quality or less available inside the refuges (Eklov and Persson 1995; Pallini et al. 1998; Martin et al. 2003b). These costs are expected to result in a lower growth rate of prey populations inside refuges. Thus, the effect of prey refuges on population dynamics of predator and prey is not obvious: escaping from predators can lead to higher prey densities, but the lower growth rate of prey inside the refuge results in lower prey densities. Moreover, the long-term population effects of refuge use cannot be extrapolated directly from these individual costs and benefits, because the growth rate of prey depends on the density of predators, which in turn depends on prey densities.

Theoretical studies have shown that the contribution of refuges to the stability of predator–prey interactions depends on numerous factors. These factors include the relative part of the population that is protected (fixed proportion vs fixed number; Crawley 1992), whether the refuge gives guaranteed protection against predators or variable, depending on predator density (absolute vs partial refuges), whether prey can reproduce inside the refuge or not, and the density dependence of prey reproduction and mortality in the refuge (McNair 1986; Sih 1987; Krivan 1997, 1998). When prey and predator are distributed over many patches (such that populations in or out of the refuge are subdivided), the parameter space for stable equilibria decreases (van Baalen and Sabelis 1993), but persistence is increased (van Baalen and Sabelis 1999). Some empirical studies have tested these predictions (Persson 1993; Eklov and Persson 1995; Caley and StJohn 1996; Schmitz et al. 1997; Rangeley and Kramer 1998). However, many systems never reach equilibrium densities, or only in the long term. For example, many herbivorous insects occur on deciduous or annual plants, thus populations are re-built every year. As a first step towards bridging the gap between theory and experiments, we have studied the short-term dynamics of a predator–prey interaction inside and outside a refuge, but without linking these compartments. In this way, we exclude the possibility of flexible behaviour in prey and in predators. We use a combined experimental and theoretical approach to study the dynamics of arthropod populations on plants with or without a refuge, and take the validated model to make predictions at longer time scales. Our experimental set-up and model are such that we disentangle the relative effect of individual costs and benefits on population dynamics.

We tested how the presence of a refuge affects the population dynamics of western flower thrips (*Frankliniella occidentalis* Pergande) and its predator, the phytoseiid mite *Neoseiulus* (=*Amblyseius*) *cucumeris*

(Oudemans). The phytoseiid mite is used as a biological control agent of thrips, which is a major pest of greenhouse crops (Gillespie 1989). The refuge used by thrips consists of the dense silken web produced by the two-spotted spider mite, *Tetranychus urticae* (Koch), a herbivore that often co-occurs with thrips in greenhouses and cultivated fields (Trichilo and Leigh 1986; Wilson et al. 1996). This web hampers predator mobility and thus reduces predator attacks on spider mites (Sabelis 1981; Gerson 1985; Sabelis and Bakker 1992) and on thrips larvae (Pallini et al. 1998; Venzon et al. 2000). Inside the web, thrips larvae compete with spider mites and with other thrips for plant tissue as a food source. Consequently, their developmental time is longer in webbed leaf areas than in unwebbed areas due to damage by spider mites (Pallini et al. 1998). Because only young and small thrips larvae are prey of *N. cucumeris* (van der Hoeven and van Rijn 1990), a longer developmental time also implies extended vulnerability to predation. Since the web is a partial refuge (i.e., predators kill prey that are in the refuge, but at a lower rate), this longer period of vulnerability is expected to increase the predation risk of prey inside the web. Therefore, using spider-mite web as a refuge does not necessarily result in higher growth rate of thrips populations, because the extension of the vulnerable period due to lower plant quality may affect the growth rate of thrips populations more than the reduction in predation rate due to web protection.

To study the effects of a refuge on the population dynamics of prey, we used a stage-structured predator–prey model with parameters tuned to the species under consideration. The predictions were validated with population experiments on plants without refuge (van Rijn et al. 2002). Subsequently, we modified these parameters to account for the effects of costs and benefits of refuge use that have been measured for individual prey (Pallini et al. 1998). By comparing model predictions with experimental results, we tested whether the costs and benefits of refuge use measured for individual prey were sufficient to explain the population dynamics in this predator–prey system. To disentangle the effect of individual costs and benefits of refuge use on population dynamics, we monitored the populations of thrips and of *N. cucumeris* on cucumber plants damaged by spider mites but without web (where thrips pay the cost of using the refuge due to a reduction in the developmental rate but gain no benefit) and on damaged plants with web (where thrips pay the cost of using the refuge but benefit through decreased predation). Moreover, we evaluated the effect of varying costs and benefits of refuge use and predator density on the population growth rate of prey,

which we take as a proxy for prey fitness. This fitness measure is valid when different genotypes within the population do not compete for resources, for example due to population structure or because the densities are low (Mylius and Diekmann 1995; Brommer 2000). Finally, we used the model to predict the long-term effect of the presence of a refuge on prey density by calculating the equilibrium densities.

Materials and methods

Greenhouse experiment

All species were cultured as described in Pallini et al. (1998). Experiments were conducted in a greenhouse compartment (9×6 m) and repeated in 2 consecutive years (1st experiment in 2002, 24°C; 2nd experiment in 2003, 21°C; approximately 70% RH in both years). Six 3-week-old cucumber plants (with three or four leaves; mean plant size 12 dm^2) were put pairwise inside three cages of $80 \times 80 \times 100$ cm. Cages were made of mite-proof gauze, except for the wooden bottom and the Plexiglas door, which was closed with strips of magnetic tape.

To create a refuge on plants, 400 spider mites were introduced on each plant, and they were subsequently eradicated by releasing 150 females of the predatory mite *Phytoseiulus persimilis* (Athias-Henriot) on each plant 4 days later. This species is a specialist predator of *Tetranychus* mites and leaves the web largely intact while foraging (Sabelis and Bakker 1992). After 8 and 14 days in the first and in the second experiment respectively, no spider mites or predatory mites were found alive, and plants were completely covered with web. To obtain plants without web but with equal amounts of spider-mite damage, the web was removed from half of the plants (one plant from each cage) by brushing all leaves and stems with a make-up brush. Subsequently, each plant was placed in a separate cage and supplied with 20 adult-female thrips. Four days later, some first-instar larvae thrips, the only stage that can be consumed by the predators, had hatched from the eggs. At this moment, 30 adult females of the thrips predator *N. cucumeris* were introduced per plant. The numbers of juvenile and adult thrips and of adult female predators on each plant were recorded twice a week. The apices of all plants were removed regularly to minimize the development of new areas without web. Experiments were carried out until 29 days after thrips release, encompassing two generations of thrips. After this

period, the plants had suffered too much from damage due to feeding by spider mites and thrips; thus the experiment was terminated. To assess the accuracy of the in situ sampling, destructive counting was performed after the last sampling; the leaves and apex of each plant were cut, and thrips (females, males, young and old larvae) and predatory mites (adults and juveniles) were counted using a stereoscope.

To test whether the presence of web affected population dynamics, we analysed data of each year with a linear mixed model using R (Ihaka and Gentleman 1996). The main factors of the model were the presence of web and the sampling day. Because populations on each plant were probably correlated among sampling events (days), we introduced an autocorrelation term in the model. Since plants were grown in pairs in cages prior to the release of thrips and predators (with each pair having one plant of each treatment), we introduced a random effect of day by cage. Data were analysed with an ANOVA on the main factors of the linear mixed model. Data from the destructive sampling were grouped over the 2 years, and comparisons between the two treatments were done using the Wilcoxon matched-pairs signed rank test (Field 2000), each pair consisting of plants from the same original cage.

The model

We used a predator–prey model based on that of van Rijn et al. (2002), in which both the prey and the predator population was structured into three age classes. Because not all stages of thrips can be observed with the naked eye, we further separated stages into visible and non-visible ones, thus allowing comparison of model predictions and experimental results. Hence, the thrips life cycle was subdivided into eggs (N_0, invulnerable, non-visible), 1st instar larvae (N_1, vulnerable, visible), 2nd instar larvae (N_2, invulnerable, visible), (pre)pupae and preoviposition females (N_3, invulnerable, non-visible), and reproducing adults (N_4, invulnerable, visible). The predator life cycle was subdivided into three stages: the first stage (P_1, eggs and larvae) is unable to attack thrips. The second (P_2, juveniles) and the third (P_3, adults) stages can attack prey, but juveniles are less efficient than adults. We therefore used a weighted predator density for predators feeding on prey $P_C = jP_2 + P_3$, with $j < 1$. This results in the following set of ordinary and delay differential equations, describing predator–prey dynamics:

$$\frac{dN_0}{dt} = RN_4(t) - RN_4(t - \tau_0)$$

$$\frac{dN_1}{dt} = RN_4(t - \tau_0) - f\left[\frac{N_1(t)}{N_1(t) + N_f}\right]$$

$$(jP_2(t) + P_3(t)) - d_1N_1(t) \qquad (1a)$$

$$\frac{dN_2}{dt} = d_1N_1(t) - d_1N_1(t - \tau_2)$$

$$\frac{dN_4}{dt} = d_1N_1(t - \tau_2 - \tau_3) - vN_4(t)$$

$$\frac{dP_1}{dt} = g\left[\frac{N_1(t)}{N_1(t) + N_g} - m\right]P_3(t) - eP_1(t)$$

$$\frac{dP_2}{dt} = eP_1(t) - eP_1(t - \tau_P) \qquad (1b)$$

$$\frac{dP_3}{dt} = eP_1(t - \tau_P) - \mu P_3(t).$$

The two stage-structured populations are linked by saturating functional and numerical responses, indicated by square brackets. Note that the equations for N_0, N_2, N_3 and P_2 are simply delays of a former stage, and do not affect the model dynamics. We included these equations (except for N_3, the hidden pupal stage of thrips) as we wanted to compare their predicted values with experimental values. Vulnerability of the larval thrips declines exponentially with age, which is well mimicked by the exponentially distributed delay between N_1 and N_2 (via the term d_1N_1). All parameters are described in Table 1.

Model results were obtained for three sets of parameters representing no refuge, the cost of refuge only and both the cost and benefit of refuge use. Under the assumption of no density or frequency dependence in the costs and benefits of refuge use, these three parameter sets describe the dynamics on clean plants without spider-mite damage or web, on damaged plants without web, and on damaged plants with web respectively. Data of population dynamics on clean plants were obtained from an independent experiment performed in 1999 in a greenhouse with 110 cucumber plants. It was used to validate the model in absence of any treatment (Fig. 1). In this experiment, plants were 5 weeks old and had 17 leaves at the beginning of the experiment; their mean size during the experiment was 45 dm². Mean temperature was 22.5°C. At day 0, 100 adult female thrips were introduced, of which 44 were assumed to have established (0.4 per plant). Ten days later, eight adult female predators were introduced on each plant, of which six were assumed to have established. The thrips population at the time of predator

Table 1 Parameter values for the stage-structured predator–prey model at 25°C

Description	Symbol	Value on clean plants	Value on webbed and/or damaged plants
Biology of thrips			
Developmental time eggs	τ_0	2.6 days	
Developmental time vulnerable larvae	τ_1 $(=d_1^{-1})$	2.3 days	3.1 days[a]
Developmental time invulnerable larvae	τ_2	3.8 days	5.1 days[a]
Developmental time pre (pupae) + pre-oviposition period	τ_3	5.5 days	
Instantaneous decline in adult net reproduction rate	v	0.14 day⁻¹	
Maximum rate of net reproduction functional response	R	2.5 adult⁻¹ day⁻¹	
Maximum predation rate	f	6 prey adult⁻¹ day⁻¹	3.1 prey adult⁻¹ day⁻¹[b]
Relative consumption by juvenile predators, relative to adults	j	0.25 (ratio)	
Prey density at which predation is half its maximum	N_f	1.5 prey dm⁻²	
Biology of N. cucumeris			
Developmental rate of eggs and larvae	e	0.33 day⁻¹	
Developmental time of nymphs	τ_P	5 days	9.7 days[b]
Maintenance costs (relative to total maintenance and reproduction)	m	0.2 (ratio)	
Maximum rate of net reproduction	g	1.85 adult⁻¹ day⁻¹	0.96 adult⁻¹ day⁻¹[b]
Prey density at which net reproduction is half its maximum	N_g	1.0 prey dm⁻²	
Adult mortality rate	μ	0.2 adults day⁻¹	

[a] On damaged plants

[b] On damaged and webbed plants

In the simulations, parameters were corrected for the temperature occurring in the greenhouse (24°C in 2002, 21°C in 2003) assuming a threshold temperature of 11°C. Data on the life-history traits of thrips were obtained fron van Rijn et al. (1995), on the functional response from van Rijn et al. (2005), on the predator traits from van Rijn and Tanigoshi (1999) and on the effects of spider-mite damage and webbing from Pallini et al. (1998). Prey density is measured as the density of vulnerable thrips larvae. See van Rijn et al. (2002) for further details
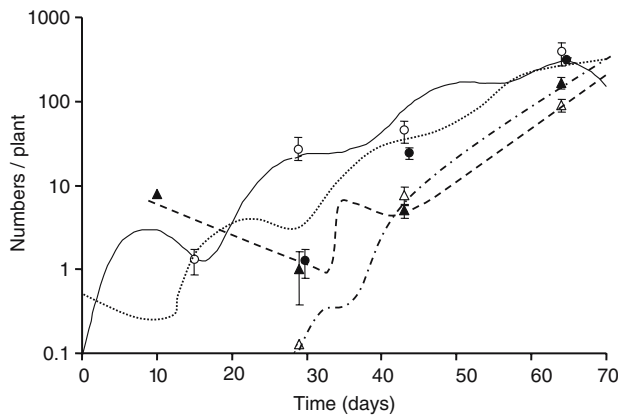
Fig. 1 Population dynamics of thrips and predatory mites on clean plants. Results are from an independent experiment in a greenhouse with cucumber plants in 1999 and used to validate the model. Experimental results are depicted by *symbols*, model calculations by *lines* (*closed circles* and *dotted lines* for adult thrips, *open circles* and *solid lines* for thrips larvae, *closed triangles* and *dashed lines* for adult predators, *open triangles* and *dashed–dotted lines* for juvenile predators). Given are numbers of thrips and predators per cucumber plant (mean and standard error over ten plants)

introduction on the plants was assumed to be in stable stage distribution with a growth rate of $r = 0.13$ day^{-1}.

The cost of refuge use was incorporated in the model by extending the developmental time of both larval stages of thrips and the benefit by reducing predation on vulnerable prey (i.e., first instar thrips larvae), based on the results of laboratory experiments by Pallini et al. (1998). Because predators that forage in the web capture fewer prey, their developmental and reproductive rates are also reduced inside this refuge. Since not all introduced predators settled on the plants, initial densities in the model were back-estimated from the numbers counted on the first two sampling dates, and these estimates were used in model simulations.

A sensitivity analysis was conducted to test whether the incorporation of individual costs and/or benefits of refuge use yielded a better fit between the model and the data. The first two sampling dates were excluded because they were used to estimate initial population sizes. Increased developmental time and reduced predator performance were either included or excluded, and the fit between model predictions and experimental data were evaluated by a lack-of-fit test (Draper and Smith 1981). For this test, the residual variance is split into the 'pure error' variance (MS$_{PE}$) resulting from spread in replicated measurements around their mean at each census, and the 'lack-of-fit' variance (MS$_{LOF}$) resulting from the deviations

between mean values and model predictions. The model is considered to give a bad fit when MS$_{LOF}$ is significantly greater than MS$_{PE}$. Under the null hypothesis the ratio:

$$F_0 = \frac{MS_{LOF}}{MS_{PE}}$$

follows an F distribution with pq and nq degrees of freedom for numerator and denominator respectively, where n is the total number of replicate measurements, q the number of levels (census) studied, and p the number of unknown parameters in the model. In our case, $p = 1$, as one parameter (the adult predator mortality, μ) was estimated on the basis of initial decline in numbers. All other parameters were estimated independently (Table 1).

In addition to our short-term simulations, more analytic insight into the consequences of costs and benefits of refuge use could be obtained from deriving equations for prey growth rate and equilibrium densities of predator and prey. The instantaneous growth rate of the thrips population (r) can be used as a fitness measure, assuming no competition or other type of density dependence between thrips genotypes. For any fixed predator density P_C, the prey population described by our stage-structured model will ultimately grow (or decrease) exponentially with an instantaneous growth rate:

$$r = \frac{dN}{dt} \times \frac{1}{N} \text{ where } N = \sum_i N_i. \quad (2)$$

This growth rate can be calculated analytically when population growth occurs for a sufficiently long time period under constant conditions (including a constant predator density), so that the stage ratios have converged towards stable values (Lotka 1922). Under this assumption, (1a) and (2) yield:

$$r = \frac{N_4}{N}(R - v) - f \frac{N_1}{(N_1 + N_f)} \frac{P_C}{N}. \quad (3)$$

When densities of vulnerable thrips larvae are low ($N_1 \ll N_f$) the population growth rate of thrips is independent of its density and can be approximated by:

$$r = s_4(R - v) - s_1 \frac{f}{N_f} P_C. \quad (4)$$

The stable stage ratios (s_1 and s_4) can be calculated as:

$$s_1 \equiv \frac{N_1}{N} = \frac{\exp[-r\tau_0] - \exp[-r(\tau_0 + \tau_1)]}{1 - \exp[-r(\tau_N + v^{-1})]}$$

$$\text{and} \quad s_4 \equiv \frac{N_4}{N} = \frac{\exp[-r\tau_N] - \exp[-r(\tau_N + v^{-1})]}{1 - \exp[-r(\tau_N + v^{-1})]}$$

(5)

where τ_N is the total developmental time ($\tau_N = \tau_0 + \tau_1 + \tau_2 + \tau_3$).

All other parameters are defined in Table 1. Because s_1 and s_4 are dependent on r and vice versa, r can only be solved implicitly by iterative methods (using a MathCad™ solve block). We explored the effect of varying predator density (P_C) and developmental time (τ_N) and the predation rate (functional response) on the growth rate r.

When prey and predator populations interact as described by (1a) and (1b) the system will converge towards equilibrium for certain parameters values. The equilibrium is stable because of the existence of invulnerable prey stages (van Rijn et al. 2002). For the parameters and initial conditions used in this paper, the system is within the 10% range around the equilibrium after ca. 150 days. The equilibrium state is described by:

$$\hat{N} = \sum N_i = \left(\frac{\tau_0 + \tau_1 + \tau_2 + \tau_3 + v^{-1}}{\tau_1}\right)\hat{N}_1,$$

$$\text{where } \hat{N}_1 = \frac{N_g(mg + \mu)}{g - (mg + \mu)};$$

(6a)

$$\hat{P} = \sum P_i = \left(\frac{e^{-1} + \tau_P + \mu^{-1}}{j\tau_P + \mu^{-1}}\right)\hat{P}_C, \text{ where}$$

$$\hat{P}_C = \left(\frac{R}{v} - 1\right)\frac{\hat{N}_1 + N_f}{\tau_1 f}.$$

(6b)

We explore the effect of varying cost and benefits of refuge use on these equilibrium densities.
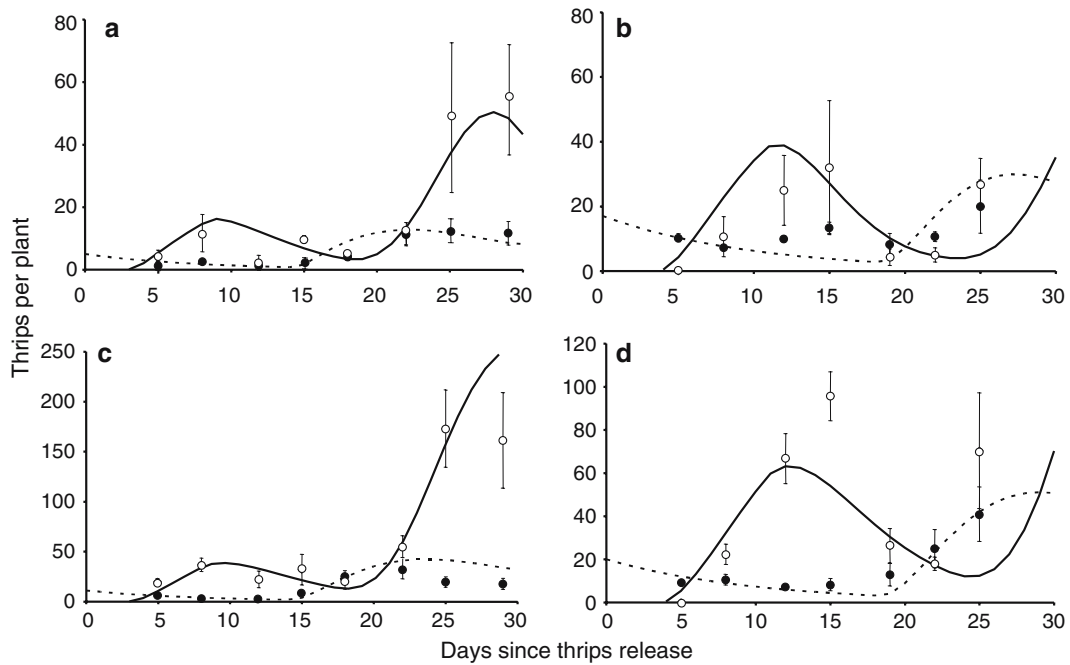
Results

Overall, more thrips juveniles were found on plants with web than on plants without web (Fig. 2; ANOVA, factor = web; 1st experiment: $F_{1,30} = 24.55$, $P < 0.0001$; 2nd experiment: $F_{1,30} = 9.28$, $P = 0.0048$). This difference increased with time (*diamonds* in Fig. 2), resulting in a significant interaction between the presence of refuge and time in both experiments (ANOVA, web × time; 1st experiment: $F_{7,30} = 3.23$, $P = 0.0113$; 2nd experiment: $F_{7,30} = 4.72$, $P = 0.0011$). Densities of juvenile thrips remained low on plants without web,

whereas they increased with time on plants with web. The number of adult thrips was also higher on plants with web than on plants without web (ANOVA, factor = web; 1st experiment: $F_{1,30} = 15.27$, $P = 0.0005$, 2nd experiment: $F_{1,30} = 5.96$, $P = 0.0207$) and this difference changed significantly with time (ANOVA, web × time; 1st experiment: $F_{7,30} = 2.37$, $P = 0.0474$, 2nd experiment: $F_{7,30} = 10.32$, $P < 0.0001$). Differences in densities of adult thrips in the two treatments became more conspicuous from day 15–18 onwards (Fig. 2, *squares*). The presence of web affected the numbers of predators in the first, but not in the second experiment (Fig. 3; $F_{1,30} = 5.27$, $P = 0.028$ and $F_{1,30} = 1.73$, $P = 0.198$ respectively). The interaction between presence of the refuge and time was not significant for predator densities (1st experiment: $F_{7,30} = 1.66$, $P = 0.158$; 2nd experiment: $F_{7,30} = 0.87$, $P = 0.536$).

Results of the destructive sampling were similar to those of the non-destructive sampling. More juvenile and adult thrips were found on plants with web than on plants without web (mean ± SEM of juveniles on plants with web: 216.3 ± 41.2; without web: 53.3 ± 15.5; Wilcoxon signed rank test, $Z = -2.2$, $P = 0.028$; adults on plants with web: 26.7 ± 6.2; without web: 13.5 ± 3.7; $Z = -1.99$, $P = 0.046$). Very few 1st instar larvae were found on all plants. Although there were a few more on plants with web, this difference was not significant (1.5 ± 0.6 on plants with web vs 0.2 ± 0.2 on plants without web; $Z = -1.63$, $P = 0.1$). Few predators were found, both on plants with web and on plants without web (7.3 ± 1.94 adults and 6.8 ± 2.95 juveniles on plants with web and 8 ± 2.91 adults and 7.66 ± 4.59 juveniles on plants without web). The presence of web had no effect on the final number of predators (Wilcoxon signed rank test, $Z = 0$, $P = 1$).

The predator–prey model was used to estimate the number of adult thrips and predators initially established (on days 0 and 4 respectively), which would fit the observations on days 5 and 8. These calculations yielded an estimation of 5 and 17 adult thrips establishing on plants without web in the first and in the second experiment respectively, and 11 and 20 respectively on plants with web. Predator numbers were estimated at 2.5 and 6.5 on plants without web and 3.8 and 10 on webbed plants in the first and in the second experiment respectively. These estimates suggest that higher numbers of thrips and predators established on plants with web than on plants without web. Therefore, the differences in prey densities between treatments during the experiments are partly due to differences in establishment of introduced thrips and mites. Model calculations were used to disentangle

Fig. 2 Population dynamics of thrips on small cucumber plants damaged by spider mites in absence (*upper panels*) and presence (*lower panels*) of webbing, in two different years: **a**, **c** 2002 and **b**, **d** 2003. Experimental results are depicted by *symbols* (*closed circles* for adult thrips, *open circles* for thrips larvae), model calculations by *lines* (*dotted lines* for adult thrips, *solid lines* for thrips larvae). *Vertical bars* correspond to standard errors of the mean ($N = 3$). Adult female thrips were introduced on day 0, adult female predators on day 4. Initial numbers used for model calculations are extrapolated from observations on days 5 and 8 (see Table 2). Note differences in scale among pannels
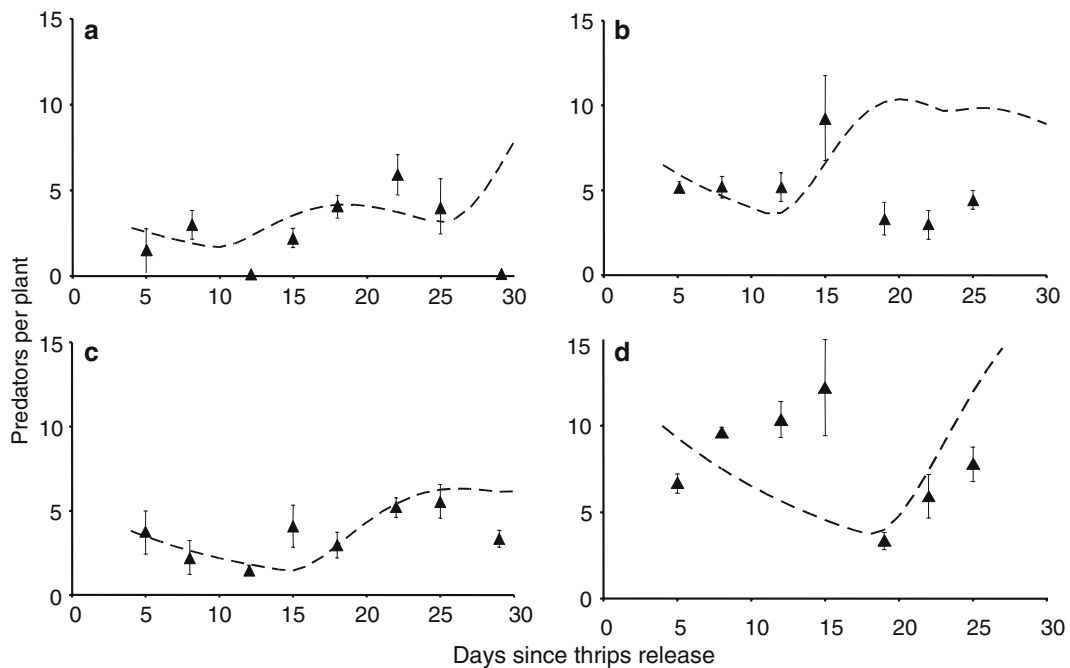
Fig. 3 Population dynamics of predatory mites on small cucumber plants in absence (*upper panels*) and presence (*lower panels*) of spider mite webbing. Data correspond to the same plants as in Fig. 2. Experiments were performed in two different years: **a**, **c** 2002 and **b**, **d** 2003. All plants were initially damaged by spider mites. Experimental results are depicted by *symbols* (*triangles*), model calculations by the *dashed lines*. *Vertical bars* correspond to standard errors of the mean ($N = 3$)

Table 2 Effects of the parameters describing costs and benefits of refuge use on the goodness of fit between model predictions and experimental data (for days 12, 15, 18, 22 and 25 of the 2002 experiment)

Removal of cost or benefit of refuge use from parameter	Lack of fit thrips larvae	(F value) Thrips adults	Predator females	Sum of F values
No web				
None (full model)	0.39	3.38	2.89	6.65
Costs: thrips development	1.25	10.80**	3.20	15.25
With web				
None (full model)	0.20	2.96	2.09	5.24
Costs: thrips development	3.16	4.91*	2.22	10.28
Benefits: Predation rate	1.64	0.57	2.48	4.69
Predator development	0.40	2.76	3.86	7.01
Predator reproduction	0.99	2.03	11.19**	14.21
All benefits	3.92	0.40	13.81**	18.12
All costs and benefits	2.39	0.50	13.58**	16.47

*/** Significant deviation between model predictions and experimental date (lack-of-fit test, $df = 5, 10$, $P < 0.05/P < 0.001$)

Parameters were systematically removed from the model, and the fit between model and data was analysed. Lack of fit indicates that the inclusion of the parameter is necessary for an accurate model description of the experimental data

this impact of the web on establishment from the impact of the web on the subsequent dynamics. Model simulations fitted well with the data of predator–prey dynamics on clean plants (Fig. 1). By incorporating a reduction in the developmental rate of thrips on damaged plants (Table 1), the population dynamics on damaged plants without web were accurately predicted (Figs. 2a, b, 3a, b; Table 2). The addition of a reduction in predation by *N. cucumeris* on thrips, and of oviposition and development rate of *N. cucumeris*, in the model yielded an accurate description of prey population dynamics on damaged plants with web (Figs. 2c, d, 3c, d; Table 2). The predator numbers were well-fitted by the model for the first experiment, but not for the second one (lack-of-fit test, $F_0(5,10) > 8$, $P < 0.01$). Leaving out one or several of these expected effects (costs or benefits) of the web refuge resulted in much worse fits between model and experiments in the first experiment (Table 2). These results indicate that the costs and benefits of refuge use for the thrips larvae as estimated in laboratory experiments are sufficient to explain the effect of the refuge on population dynamics during the initial phase of the predator–prey interaction.

When taking equal initial numbers of thrips and of predators in the two treatments, the model predicts that numbers of thrips (adults and 2nd instars) on day 22 would be 1.6–1.9 times higher with web than without web when choosing the initial numbers for the first experiment, or 2.1–2.2 times higher with the initial numbers for the second experiment. Without damage inflicted by spider mites, the web refuge would result in a 2.9- to 3.2-fold increase in thrips numbers. Therefore, the web had an effect on the populations of thrips and

their natural enemies in two ways: it affected their establishment as well as their subsequent population dynamics.

The model predicted that the effect of the refuge on prey population growth rate varies with predator density (Fig. 4a). At low predator densities, the prey population growth rate is higher outside the refuge than inside, due to better food quality of leaf tissue without damage and web. With increasing predator densities, the growth rate of the prey population decreases, but it does so at a higher rate outside the refuge than inside. Above a critical predator density P_k, the prey population growth rate is higher inside the refuge. Under the experimental conditions, predator densities (jP_2+P_3) were always above P_k (0.16 predators dm^{-2}, Fig. 3), thus the population growth model predicts that thrips densities should be higher in presence than in absence of the refuge.

To test how different values of individual costs and benefits of refuge use affected our results, we varied them using the model, and measured their impact on the instantaneous growth rate of prey populations (Fig. 4b). In absence of predators ($P_C=0$, upper lines), refuge use entails only costs (reduced developmental rate) and yields no benefits (reduced predator performance). Indeed, the upper curve for costs and benefits together (*solid line*) is confounded with that of costs only (*dotted line*) and the line of benefits only is horizontal. With increasing predator densities (and consequently lower growth rates, cf. *Y*-axis), the benefit of refuge use increases. At the critical predator density P_k (*intermediate lines*), benefits and costs are balanced and the prey growth rate is equal in presence and in absence of a refuge (at $X = 1$ and $X = 0$, respectively). At
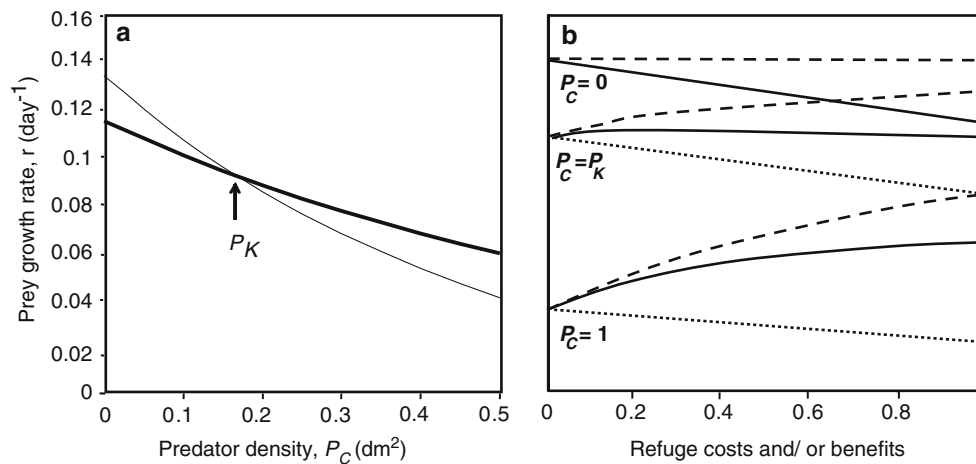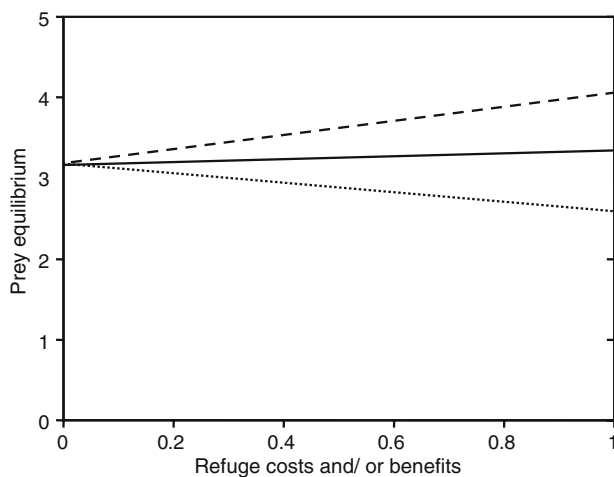
Fig. 4 Effects of predator density and of refuge costs and benefits on the instantaneous prey population growth rate (r). **a** Effect of predator density on thrips population growth rate in absence (*thin line*) and presence (*thick line*) of a web refuge. Beyond the critical predator density (P_k) thrips benefit from using the refuge. **b** Effect of refuge use on thrips population growth rate when only costs (reduced development, *dotted lines*), or benefits (reduced predator consumption and reproduction, *dashed lines*) or both (*solid lines*) are incorporated in the model. Shown are the effects for three different predator densities: P_C

($=jP_2+P_3$) $= 0$, *upper lines* (note that the *dotted line* is confounded with the *solid line*); 0.16, *intermediate lines* and 1/dm², *lower lines*. Costs and benefits are scaled in such a way that 1 indicates the expected value (Table 1). $X = 0$ corresponds to the absence of a refuge. $P_C = 0.16$ predators/dm² corresponds to the critical predator density (P_k) at which the expected costs and benefits equal out in terms of their impact on the growth rate of prey populations. Calculations are based on the equations for the prey population and on parameters of Table 1 (corrected for temperature = 23°C)

predator densities above P_k ($P_C = 1$, *lower lines*), the benefits of refuge use outweigh the costs, resulting in higher values of prey growth rate in presence of the refuge. Overall, the effect of varying costs and benefits of refuge use on prey growth rate are rather low,

Fig. 5 Effects of refuge costs (reduced development, *dotted line*), or benefits (reduced predator consumption and reproduction, *dashed line*), or both (*solid line*) on equilibrium thrips density according to the predator–prey model and to parameters in Table 1 (corrected for temperature = 23°C). Costs and benefits are scaled in such a way that 1 indicates the expected value inside the web (see Table 1)

especially compared to the effect of varying predator density.

Model analysis shows that the predator–prey system converges towards equilibrium in many cases (see also van Rijn et al. 2002). Equilibrium calculations, independent of arbitrarily-chosen initial conditions, can extend our knowledge on the overall effect of a refuge on predator–prey dynamics. Such calculations show that refuge costs reduce the prey equilibrium only due to the extended vulnerability to predation (longer developmental time in vulnerable thrips larvae, τ_1). They also show that the only benefit associated to refuge use that affects the thrips equilibrium is the lower predator reproduction rate (g). The effect is rather small, and the overall effect of costs and benefits of refuge use is only a slight increase of prey density at equilibrium (Fig. 5).

Discussion

Populations of thrips were larger on plants with web produced by two-spotted spider mites than on plants without this refuge. This was in part due to differences in establishment of adult thrips, suggesting that thrips accept plants with web more readily than plants without web. Predators also settled more frequently on plants with web, probably as a consequence of higher

initial numbers of thrips on those plants. However, the model exercise and the significant interaction between the presence of web and time indicated that the subsequent dynamics of populations of thrips were also affected by the presence of the refuge, independently of the initial effect. Differences in the numbers of adult thrips on plants with or without web increased from days 15–18 onwards in the two replicates. This period is roughly equal to the generation time of thrips (van Rijn et al. 1995), suggesting that the effect of the refuge on the adult thrips population was a consequence of the reduced predation on young thrips ca. 2 weeks earlier. The final density of predators was not affected by the presence of web. The model predicted that the density of the vulnerable prey (1st instar larvae) was fluctuating near the critical value that just allows for a positive growth rate of the predator population on the two treatments (4 larvae/plant in absence of web, 8.1 larvae/plant in presence of web—a higher number is required in this case because a smaller fraction of the prey population is available to the predator). These densities are not exceeded in our experiments. Therefore, predators are probably limited by food in both treatments.

Model simulation yielded a good fit with the data of population dynamics on damaged plants without web (where prey only pay the cost of using the refuge) and on damaged-and-webbed plants (where prey pay the cost but yield the benefit of using the refuge). A sensitivity analysis (Table 2) showed that incorporating in the model the individual costs and benefits measured in an independent laboratory experiment (respectively, a reduction in the developmental rate and a reduction in predator performance) is essential for the goodness of fit observed. This showed that individually measured costs and benefits of refuge use can be extrapolated to the population level, at least for the timescale of our experiments.

The model-derived population growth rate indicated that prey have higher growth rates inside the refuge than outside whenever predator densities exceed 0.16 predators/dm^2 (P_k, Fig. 4). This density is often surpassed in greenhouses where $N.$ $cucumeris$, thrips and spider mites co-occur (Gillespie 1989; Steiner 1990; Brødsgaard and Hansen 1992; Higgins 1992; van Houten and van Stratum 1995; Castineras et al. 1997; De Courcy Williams 2001; Jacobson et al. 2001). Thus, we would expect higher growth rates of thrips in greenhouses with webbed plants.

Greenhouse crops are typically seasonal, transient systems. At this temporal scale, our results show a strong effect of the presence of a refuge on the populations of thrips and their predators. However, if the interaction lasts long enough to approach equilibrium, the model predicts that the effect of the refuge on prey dynamics will be small (cf. Fig. 5), due to feed-back with predator population size. Other factors may affect population dynamics of this system in the long term. Both herbivores affect plant quality (Vanimpe and Hance 1993; Hao et al. 2002), which in turn will affect herbivore populations. Moreover, the refuge has dynamics of its own, because it is built by spider mites. The growth of spider-mite colonies is affected by competition with thrips, but also by intraguild predation of thrips on eggs of spider mites (Trichilo and Leigh 1986; Agrawal et al. 1999; Magalhães et al. 2005). These interactions will, in turn, affect the population growth of thrips. Moreover, $N.$ $cucumeris$ may also feed on spider mites (Easterbrook et al. 2001). This system is thus characterized by the occurrence of complex interactions such as intraguild predation and apparent competition, which are likely to affect the growth of thrips populations both inside and outside of the refuge. To be able to infer processes from the patterns observed, we have reduced the complexity and excluded many of these interactions by excluding the spider mites from our experimental design. In future studies, a (gradual) extension to include the full complexity of the system will certainly add to our understanding of how complex interactions shape the behaviour of individuals and affect the dynamics of populations.

Entering a spatial or habitat refuge is one way to (partially) escape predation; growing to an invulnerable stage ('prey size' or 'developmental' refuge) is another one (Murdoch et al. 1987; Chase 1999; de Roos et al. 2002; Persson and de Roos 2003; Arendt and Reznick 2005). In our experimental system both types of refuge are present, and, interestingly, there is trade-off between them. Indeed, thrips larvae within a web (or habitat refuge) experience a slower development due to reduced food quality. This in turn leads to a longer developing time, resulting in an extension of the vulnerable stage 1st instar. Thrips larvae that feed on food of better quality outside the refuge can grow faster to their invulnerable stage, but they will temporarily experience higher predation risks (van Rijn et al. 2002). Therefore, prey may face a dilemma of growing faster or using a habitat refuge. By calculating separate impacts of the costs and benefit of refuge use on prey population growth rate, we showed that the benefits of a web refuge are higher than the costs, including the extended vulnerability, provided that the predator density is sufficiently high. We also suspect that the temporal patterns of predation risk (e.g., regular vs sporadic, predictable vs unpredictable)

may affect which of the two strategies (spatial refuge vs size refuge) will be more advantageous. Further analysis is needed to assess this.

A refuge will only be useful when there is predation risk, and the higher the cost of refuge use, the higher the predation risk should be before refuge use will become profitable (Fig. 4). Our expression for prey population growth rate (which can be used as a proxy for fitness) allows us to calculate the critical predator density where costs and benefits of refuge use cancel out. This calculation provides a prediction that can be tested in an independent behavioural experiment. Prey that behave optimally in this framework should prefer non-refuge areas when predator density is below this critical value, and should move into refuges otherwise (Fig. 4). In our experimental set-up, thrips were on plants either with or without web, but they were not given the choice between these types of plants. One important extension of our analysis therefore is to offer prey a choice between areas with or without a refuge, such that prey can display flexible behaviour in response to predators. Since the refuge is not absolute, predator density in areas with or without refuge is expected to vary in response to prey density as well. This, in turn, will affect the relative prey availability on each area. Therefore, the consequences of both prey and predator flexible behaviour should be further evaluated in population experiments. A predator–prey model that incorporates this flexible behaviour could thus be validated, and used to analyse the consequences for stability and persistence (Krivan 1997; van Baalen and Sabelis 1999). This may help to further narrow the gap between models and experiments (see e.g., Skalski and Gilliam 2002; Vos et al. 2004).

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