

Patch residence time and patch preference of the predatory mite *Amblyseius swirskii* in relation to prey diversity

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Abstract Patch-related behaviour of a generalist predator may be influenced by patch prey diversity and result in more time being spent in patches with more than one prey species to increase the benefits of mixed diet. To examine if generalist predators are able to discern differences in prey diversity in and among patches, we examined the patch-related behaviour of the predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae). Three lab experiments using clean, single-prey or mixed-prey patches were conducted, using whiteflies and spider mites as prey. The experiments were: (1) patch leaving tendency and residence time in absence and (2) presence of another patch, (3) patch preference. *A. swirskii* recognized prey-inhabited patches from a distance and showed a preference for mixed-prey patches over single-prey patches. The patch-related behaviour of *A. swirskii*,

which seems tuned to exploiting the fitness gains of a mixed diet, is influenced by both local and distant cues.

Keywords Optimal foraging theory · *Trialeurodes vaporariorum* · *Tetranychus urticae* · Phytoseiidae · Biological control · Patch leaving tendency

Introduction

The whitefly *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) and the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) are economically important pests in many crops in greenhouses worldwide (Gerling 1990; Helle and Sabelis 1985). Biological control of both pest species with various natural enemies has been practiced in greenhouse crops for many years (Helle and Sabelis 1985; Inbar and Gerling 2008; McMurtry et al. 2013).

The polyphagous predatory mite *Amblyseius swirskii* (Athias-Henriot) (Acari: Phytoseiidae), having the advantage of being able to control both pest species (e.g. Cock et al. 2010; van Houten et al. 2007) as well as others (e.g. Arthurs et al. 2009; Bolckmans et al. 2005; van Maanen et al. 2010), has in the last decade increased in importance as a biocontrol agent. It is currently released in more than 50 countries, especially for control of greenhouse pests (Messelink et al. 2006; Nomikou et al. 2001).

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Many aspects of the biology of *A. swirskii* have been investigated, including life table parameters (Abou-Elella et al. 2013; El-Laithy and Fouly 1992; Fouly et al. 2011; Ji et al. 2013), predation rate and fecundity (Arthurs et al. 2009; Bolckmans et al. 2013; Ragusa and Swirski 1977), functional response (Midthassel et al. 2014; Xiao et al. 2013), temperature requirements (Lee and Gillespie 2011), compatibility with other biocontrol agents (Calvo et al. 2009; Chow et al. 2010), prey preference (van Maanen and Janssen 2008; Xu and Enkegaard 2010) and intraguild predation (Momen and Abdel-Khalek 2009; Sato and Mochizuki 2011). However, aspects relating to patch finding and patch leaving behaviour and patch preferences have not been studied for this predator. Studies on patch-related behaviour are also scarce for other predators exploited in biological control (Vanas et al. 2006).

The optimal foraging theory predicts that dietary selections of a predator should increase its net nutritional gain while decreasing costs and predation risks (Stephens et al. 2007). To maximize their fitness predators need to make optimal decisions on the time spent in a patch and when to leave it in search for new ones (Charnov 1976; Maeda and Takabayashi 2001; Vanas et al. 2006). Once a patch has been chosen, the residence time of a predator may be affected by conditions both outside and within the patch (Dicke and Vet 1999). Thus, volatiles emitted from pest-infested plants outside of a patch have been shown to influence patch residence time (Maeda et al. 1998), and among within-patch influences, density levels of both prey and conspecifics (Bernstein 1984; Takafuji 1977) as well as the presence of prey products (faeces, exuviae, webs) (Maeda and Takabayashi 2001) influence predator emigration rate. When dealing with generalist predators, prey diversity in a patch might influence patch-related behaviour based on the assumption that generalist predators will spend more time in high-diversity patches to benefit from the positive effects of mixed diet in terms of, for example, increased fecundity, juvenile survival, development rate and population growth (Messelink et al. 2008). A positive effect in terms of a significantly increased fecundity of *A. swirskii* fed on mixed diet of spider mites and whiteflies compared with single-species diets has been found recently (S. Heydari, unpublished data). It is, however, still unclear whether generalist predators are able to discern differences in prey

diversity in and among patches. Based on these considerations, the effects of prey diversity on the patch-related behaviour of *A. swirskii* were investigated in three experimental set-ups: (1) residence time in patches with different prey diversity in absence of other patches, (2) residence time in patches with different prey diversity in presence of another patch, (3) patch preference when given a choice between patches of different prey diversity.

Materials and methods

Plants, insects and mites

Cucumber plants (*Cucumis sativus* L., var. Viking) were produced in plastic pots (12 cm diameter, 12 cm height) in a climate-controlled greenhouse room at 25 ± 2 °C, 50–70% RH and L:D 16:8 at Research Centre Flakkebjerg, Aarhus University, Denmark. Spider mites (*T. urticae*) and greenhouse whiteflies (*T. vaporariorum*), originating from long-standing cultures at Aarhus University, were reared separately on cucumber in net-covered cages (61 × 66 × 75 cm) in a glasshouse at similar conditions as above. *Amblyseius swirskii* was supplied by Borregaard Bioplant, Denmark. *A. swirskii* was reared on the factitious prey mites provided in the product as food source. Rearing was done in plastic boxes (20 × 15 × 5 cm) kept in growth chamber at 25 ± 1 °C, 50–70% RH and L:D 16:8. To obtain predators of uniform age, *A. swirskii* eggs were collected every second day and transferred to a new box. After 8–10 days, females were collected and kept for starvation. Starvation took place on clean cucumber leaf discs each surrounded with a thin cotton roll folded over the edges and placed upside down on a filter paper-covered and water-saturated sponge in a plastic tray half filled with water. Starvation took place for 10–14 h after which the females were used for experimentation.

Experimental set-up

All experiments were carried out using cucumber leaf discs (15 mm diameter) placed upside down on a water-saturated sponge covered with moist filter paper in a plastic tray half filled with water. A thin cotton roll was folded over the edges of the leaf disc to keep it

alive and turgid and to prevent mites from escaping (Vanas et al. 2006). Each arena carried a defined number of spider mite nymphs (protonymphs) and/or whitefly nymphs (first instars) (see below), which are the preferred prey stages for *A. swirskii* (unpublished data). Whitefly infested leaf discs were produced by introducing large numbers of adult whiteflies to clean cucumber plants kept in net-covered cages for a 24 h oviposition period after which adults were removed. The plants were kept in the climate-controlled greenhouse room until first instar nymphs had developed. Leaf discs were then cut from the leaves and examined under a stereo microscope to remove excess nymphs as well as eggs and nymphs that had progressed beyond the first instar stage. Spider mite infested leaf discs were obtained by transferring protonymphs with a fine brush either to clean leaf discs or to leaf discs harboring first instar whitefly nymphs. All leaf discs were prepared immediately prior to their use in the experiments. Consequently virtually no, if any, honey dew or webbing occurred on the leaf discs. All the experiments took place under laboratory conditions (23 ± 1 °C).

Patch leaving tendency and residence time in absence of other patches

To investigate the patch leaving tendency and residence time of *A. swirskii* in patches of different diversity, we used an experimental set-up consisting of a leaf disc carrying either no prey (clean leaf, treatment “C”), eight *T. urticae* (treatment “S”), eight *T. vaporariorum* (treatment “W”) or four *T. urticae* and four *T. vaporariorum* (treatment “WS”). The leaf discs were prepared just prior to the addition of a single *A. swirskii* female on the middle of each disc. After 30 min of acclimatization, the prey density on the leaf discs was checked. If density had changed during acclimatization (due to predation events), the replicate was discarded (three replicates were discarded in this experiment). Subsequently, a small opening was made in the cotton edge and a parafilm bridge (30 mm length, 3 mm width) connecting the rim of the leaf disc to the exterior was established. The mite was subsequently observed for 30 min. Predatory mites that left the leaf disc and reached the far end of the bridge within the observation period were defined as patch leaving mites and their residence time recorded. In addition, the number of attempts to leave

the patch was scored by recording the number of times a predator reached the edge of the patch. Each treatment was replicated 20 times, with all replicates having unaltered density on the leaf discs when observations commenced.

Patch leaving tendency and residence time in presence of another patch

To investigate the patch leaving tendency and residence time of *A. swirskii* in patches of different diversity in the presence of another patch, we used an experimental set-up consisting of two leaf discs connected by a parafilm bridge of dimensions as described above. Prior to the initiation of the experiment, the bridge openings onto each leaf disc were blocked by the cotton roll edges. Each of the discs carried whiteflies, spider mites or both pest species in the same number as stated for the previous experiment. The leaf discs were prepared just prior to the addition of a single *A. swirskii* female on the middle of one of the disc (“starting disc”). After 30 min of acclimatization, the prey density on the starting discs was checked. If density had changed during acclimatization (due to predations), the replicate was discarded (three replicates were discarded in this experiment). Subsequently, the two leaf discs were connected by removing the cotton roll coverings of the bridge openings onto each leaf disc. The mite was subsequently observed for 30 min. The following combinations of prey species on the two leaf discs were used: (1) whiteflies in contrast with spider mites, (2) whiteflies and spider mites in contrast with spider mites, (3) whiteflies and spider mites in contrast with whiteflies, (4) clean leaf in contrast with spider mites, (5) clean leaf in contrast with whiteflies and (6) clean leaf in contrast with whiteflies and spider mites. For each combination, two treatments were possible. For example, for whiteflies in contrast with spider mites in one treatment the predatory mite was placed on the disc with whiteflies and in the other on the disc with spider mites. Thus a total of 12 treatments were made, each with 20 independent replications, all of which with unaltered density on the starting discs when observations commenced. The position of the leaf disc initially harbouring the predatory mite was switched between replications to prevent any unforeseen asymmetry in environmental factors during the experiments. Recordings were made as in the previous

experiment with patch leaving mites being defined as mites crossing the bridge and reaching the other patch.

Patch preference

To investigate the patch preference of *A. swirskii* between two patches with different prey diversity, we used an experimental set-up consisting of two leaf discs connected by a parafilm bridge as described above. Each of the discs carried the same number of pest individuals as stated for the previous experiments. The experiment was started by placing a single *A. swirskii* female on the middle of the bridge. After 30 min of acclimatization, the cotton roll coverings of the bridge openings onto each leaf disc were removed to connect the two discs. The mite was subsequently observed for 30 min. The combinations of prey species on the two leaf discs were as described in the previous experiment with each of the six treatments being replicated 30 times. Position switching of discs took place as described above. Predatory mites that left the bridge and chose one of the patches within the 30 min observation period were defined as showing preference.

Statistical analysis

Three different statistical models were used to model 1) the number of attempts to leave the leaf disc made by the predator, 2) the time for the predator to leave the leaf disc and 3) the probability of the predator choosing between the two patches. The inference with these three models was performed using the software R (R Development Core Team 2013).

The number of attempts to leave the leaf made by the predator was described by a Poisson model for counts. More precisely, we used a generalized linear model defined with the Poisson distribution as described in McCullagh and Nelder (1989) and Jørgensen et al. (1996) (implemented in the function `glm` of the R-package `stats`) using the Poisson distribution and the identity link function. Formal hypothesis tests for counts (e.g. simultaneously testing equality of treatment effects) were performed by using standard likelihood ratio tests.

A Cox hazard proportional model with discrete time was used to analyse the time for a predator to leave the leaf disc, which is a classical model that takes into account that some of the observations are right

censored, i.e. some observations are only known to be larger than 30 min (Kalbfleisch and Prentice 2002; Maia et al. 2014; see also Cox 1972). These models were adjusted by exploring the coincidence of the likelihood function of the Cox proportional hazard model with discrete time and the likelihood function of a generalized linear model with binomial distribution and logarithmic link to a suitably constructed pseudo-data set representing the occurrences of the events (staying or leaving the leaf discs) at each time (see Maia et al. 2014 Sect. 3.1 page 1291 for details). The assumption of proportionality of the hazard functions, implicitly made in the Cox proportional model, was formally tested by testing (by the likelihood ratio test) the presence of interaction between the treatments and the explanatory variable representing the baseline (i.e. the time development of the hazard function). No evidence of deviations from the hazard proportionality assumption was found (result not shown). To obtain a simple quantification of the time for a predator to leave the leaf disc, we reported the median time, which was less than 30 min (with the exception of one case) and therefore this estimate was not distorted by the presence of right censure. Confidence intervals for the median were obtained by using non-parametric bootstrap (see Davison and Hinkley 1997) with 10,000 bootstrap repetitions.

The probability of the predator choosing between two choices offered was modelled using binomial models for proportions. More precisely, we used a generalized linear model defined with the binomial distribution and the logit link function. Likelihood ratio tests for generalized linear models were used to perform formal hypothesis tests comparing proportions. The Fisher exact (Agresti 1990 and Jørgensen et al. 2012) was used for testing equality of the probabilities of selecting either choice in Table 3.

Results

Patch leaving tendency and residence time in absence of other patches

A. swirskii reacted differently when introduced into different prey patches in terms of attempts to leave (Fig. 1). A likelihood ratio test based on a Poisson model for counts revealed that the mean numbers of attempts were not all equal ($\chi^2 = 45.257$, $df = 3$,

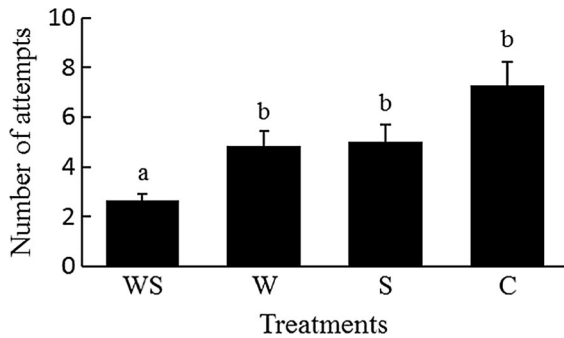


Fig. 1 Mean number of patch leaving attempts (+ SE) made by *Amblyseius swirskii* when placed on leaf discs harbouring different prey (treatments: C: clean leaf, S: spider mites, W: whiteflies, WS: whiteflies and spider mites). Different letters indicate statistically significant differences at a 5% significance level (using P-values adjusted by the False Discovery Rate method according to Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001))

$P < 0.0001$). Pairwise comparisons indicated that while *A. swirskii* was significantly less likely to leave patches simultaneously harbouring both pest species, no significant differences were found among the other treatments (Fig. 1). These results suggest that *A. swirskii* prefers mixed-prey patches over patches with no prey or with one prey species present.

The response of *A. swirskii* to the different prey patches expressed as hazard ratios differed statistically among treatments ($\chi^2 = 102.78$, $df = 3$, $P < 0.0001$) (Table 1). When it was presented with whiteflies and spider mites simultaneously, the hazard ratio was reduced to only 4% of that observed in response to clean leaves, which was also reflected in the substantial increase in the median residence time (more than

half of the leaving times were longer than the observational period of 30 min) (Table 1). The hazard ratio for the treatments with clean patches (reference treatment with hazard ratio 1.0) was significantly higher than hazard ratios of each of the other treatments. Moreover, no statistically significant differences were found between the hazard rates of the treatment with only whiteflies (hazard ratio of 0.14 and 95% confidence interval, 0.07–0.30) and the treatment with only spider mites (hazard ratio of 0.13, 95% confidence interval, 0.06–0.28). The hazard ratio of the treatment with whiteflies and spider mites was estimated as 0.04 (95% confidence interval, 0.01–0.11), which is lower than the estimates of the hazard ratio for the treatments with only whiteflies or only spider mites, although these differences were only suggestive (adjusted P-values close to 0.05). Table 1 displays the details of this analyses, including the median residence time, estimates of the hazard ratios (with respective confidence intervals) and all the pairwise comparisons between the hazard ratios (adjusted by the False Discovery Rate method as described in Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001) and implemented in the function “p.adjust” in R software).

Patch leaving tendency and residence time in presence of another patch

When *A. swirskii* was initially placed in a prey patch and had the opportunity to move to another patch with a different prey composition, it reacted differently in terms of attempts to leave (Fig. 2). The likelihood

Table 1 Estimated hazard ratio and median residence time (min) of *Amblyseius swirskii* in patches harbouring different prey (treatments: C: clean leaf, S: spider mites, W: whiteflies, WS: whiteflies and spider mites)

Treatment	Hazard ratios * (95% CI)	Median residence time	Pairwise comparisons		
			W	S	WS
C	1.00 ^a (reference)	8.0 (6.5–9.0)	<0.001	<0.001	<0.001
W	0.14 ^b (0.07–0.30)	25.5 (14.0–25.5)		1.00	0.059
S	0.13 ^b (0.06–0.28)	23.5 (18.0–23.0)			0.069
WS	0.04 ^b (0.01–0.11)	>30			

P-values for the pairwise comparisons between hazard ratios between the treatments adjusted by the False Discovery Rate method for controlling false (Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001), implemented in the function “p.adjust” in the R software). Wald confidence intervals (CI) with 95% coverage for the hazard ratios and non-parametric bootstrap confidence intervals for the medians (10,000 bootstrap simulations) are given in parentheses

*Values followed by the same letter (a, b) are not statistically significant at a 5% significance level

ratio test based on a Poisson model for counts revealed that the mean numbers of leaving attempts of predators subjected to the different treatments were not all equal ($\chi^2 = 110.34$, $df = 11$, $P < 0.0001$). Pairwise comparisons showed the number of leaving attempts to be influenced by the prey composition on the starting patch (Fig. 2), with the two extreme ends of the continuum being represented by treatments offering a mixed-prey patch in combination with a clean leaf (treatment WS–C and C–WS). Not surprisingly, *A. swirskii* was more likely to leave initial patches with no prey in favour of patches with prey (treatment C–W, C–S and C–WS), than it was to leave patches harbouring prey in favour of clean leaves (treatment WS–C, W–C and S–C), or harbouring mixed prey in favour of single-prey patches (treatment WS–W and WS–S) (Fig. 2). The latter could indicate a higher tendency for the predator to remain in mixed-prey patches instead of moving to single-prey patches although this was not reflected in significantly higher leaving attempts from single-prey patches to mixed-prey patches in treatments W–WS and S–WS (Fig. 2). The predator was also more likely to leave an initial single-prey patch in favour of another single-prey patch (treatment S–W and W–S) or an initial single-prey patch in favour of a mixed-prey patch (treatment W–WS and S–WS) than it was to leave an initial

mixed-prey patch in favour of a clean leaf (treatment WS–C) (Fig. 2).

As was the case with the hazard ratios in the experiment where no other patches were present, the ratios differ statistically among the twelve treatments ($\chi^2 = 48.096$, $df = 11$, $P < 0.0001$) where *A. swirskii* had the opportunity to move from an initial to an alternative patch (Table 2). The ratios mimicked the patch leaving tendency (Fig. 2). Thus the hazard ratio in treatments where predatory mites could move from mixed-prey patches to clean patches (treatment WS–C) was just one-fifth of the hazard ratio observed in treatments involving movements from initial clean patches to mixed-prey patches (treatment C–WS), again reflected in a substantial increase in residence time (more than half of the times to leave the path were longer than the observational period of 30 min) (Table 2). A group of treatments had significantly lower hazard ratios compared with the remaining treatments: all initial mixed-prey vs. alternative clean patch or single-prey patch treatments (WS–C, WS–S and WS–W) plus the treatment initiating predators on a whitefly patch with the possibility to choose a clean patch (W–C) (Table 2). No significant differences were found among the remaining treatments (P-values adjusted by the False Discovery Rate method as described in Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001)).

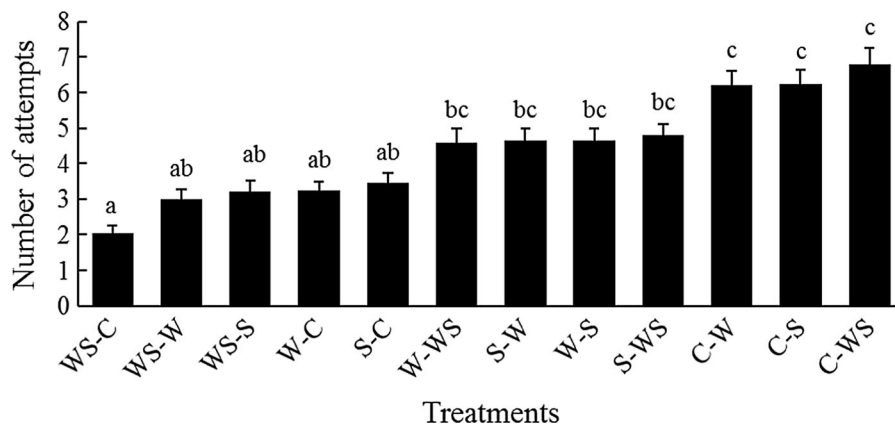


Fig. 2 Mean number of patch leaving attempts (+ SE) made by *Amblyseius swirskii* when placed on a leaf disc harbouring a specific prey and connected to another leaf disc harbouring a different prey (C: clean leaf, S: spider mites, W: whiteflies, WS: whiteflies and spider mites). The abbreviation mentioned first for each treatment denotes where predators were placed at the onset of the experiment, for example in treatment WS–C

predators were placed in a mixed-prey patch connected to a patch with no prey. Different letters indicate statistically significant differences at a 5% significance level (using P-values adjusted by the False Discovery Rate method according to Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001))

Table 2 Estimated hazard ratio and median residence time (min) of *Amblyseius swirskii* when placed on a leaf disc harbouring a specific prey and connected to another leaf disc harbouring a different prey (C: clean leaf, S: spider mites, W: whiteflies, WS: whiteflies and spider mites)

Treatment	Hazard ratio (95% CI)*	Median residence time
C-WS	1.00 ^a (reference)	4.5 (2.0–6.0)
C-W	0.97 ^a (0.53–2.13)	5.5 (3.0–6.0)
C-S	0.94 ^a (0.51–2.05)	5.0 (4.0–6.0)
W-WS	0.44 ^{ab} (0.16–0.68)	17.0 (12.0–18.0)
S-W	0.43 ^{ab} (0.17–0.77)	20.0 (14.0–22.0)
W-S	0.38 ^{ab} (0.22–0.92)	20.0 (16.0–22.0)
S-WS	0.34 ^{ab} (0.09–0.43)	15.5 (11.0–17.0)
S-C	0.31 ^{ab} (0.11–0.53)	27.0 (24.0–27.5)
W-C	0.24 ^b (0.11–0.52)	28.0 (24.0–29.0)
WS-S	0.23 ^b (0.12–0.53)	27.0 (23.5–28.0)
WS-W	0.23 ^b (0.20–0.83)	27.5 (24.0–28.5)
WS-C	0.18 ^b (0.23–0.97)	>30.0

The abbreviation mentioned first for each of the twelve treatments denotes where predators were placed at the onset of the experiment, for example in treatment “WS–C” predators were placed in a mixed-prey patch connected to a patch with no prey. Wald confidence intervals (CI) with 95% coverage for the hazard ratios and non-parametric bootstrap confidence intervals for the medians (10,000 bootstrap simulations) are given in parentheses

*Values followed by the same letter (a, b) are not statistically significant at a 5% significance level obtained with P-values adjusted by the False Discovery Rate method (Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001), implemented in the function “p.adjust” in the R software). Wald confidence intervals (CI) with 95% coverage to the hazard ratios are given in parentheses

Patch preference

When presented with a choice between patches with different prey combinations, *A. swirskii* showed significant preference in four out of six choice setups (Table 3) with the probability of selecting the first choice and the probability of selecting the second choice differing significantly at the level of significance of 5% according to a binomial exact test (see Conover (1971)) (the P-values adjusted by the False Discovery Rate method as described in Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001) are displayed in Table 3). Thus the predator chose patches harbouring any prey over clean patches (treatments S vs. C, W vs. C and WS vs. C) indicating that *A. swirskii* recognize prey-inhabited patches from a distance. The mites also chose mixed-prey patches

over patches with spider mites (treatment WS vs. S) but did not show any preference between single-prey patches (treatment S vs. W) or between mixed-prey patches and patches with whiteflies (treatment WS vs. W), although there was a tendency to choose the mixed-prey patch in the latter treatment (adjusted *P* value = 0.099) (Table 3).

Discussion

Patch leaving tendency and residence time in absence of other patches

A. swirskii had a lower tendency to leave mixed-prey patches compared with single-prey or clean patches and had longer residence times in patches with prey, independent of prey diversity. Although prey density *per se* was not studied here, the results are in accordance with the prey density-dependent dispersal reported for other phytoseiid mites (Bernstein 1984; Maeda et al. 1998; Takafuji 1977) which increase residence time in patches with high prey density in response to the presence of both prey and prey-related cues (Maeda and Takabayashi 2001; Mayland et al. 2000). The fact the generalist predatory mite, *A. swirskii*, reacted in a similar fashion as the specialist phytoseiid mites (*Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus* [*Amblyseius*] *womersleyi*) in the mentioned studies indicates that assessment of the local resource level of a particular patch as a part of the decision process on whether or not to leave the patch (Maeda et al. 1998; Maeda and Takabayashi 2001; Mayland et al. 2000) is a general phenomenon in phytoseiids, irrespective of prey specialization. For *A. swirskii* the tendency to a difference in hazard ratios between single-prey and mixed-prey patches could indicate that it perceives diverse patches as being more rewarding than uniform patches.

Patch leaving tendency and residence time in presence of another patch

When *A. swirskii* had the opportunity to move from an initial patch to an alternative patch with a different prey composition, the results mimicked those found in the previous experiment in the sense that the tendency to leave mixed-prey patches was lower than the tendency to leave clean patches, and that the longest

Table 3 Number of times (out of 30) the first choice was selected by the *Amblyseius swirskii* when given a choice between two patches with different prey composition, together with the P-value testing equality of the probabilities of selecting either choice (Fisher exact test; P-values adjusted

by the False Discovery Rate method according to Benjamini and Hochberg (1995) and Benjamini and Yekutieli (2001)) and a 95% Cloper-Pearson confidence interval for the probability of selecting the first choice

Treatment	First choice	Number of first choices	Adjusted P-value	95% CI
S vs. C	S	22	0.016	(0.54–0.88)
W vs. C	W	23	0.005	(0.58–0.90)
WS vs. C	WS	23	0.005	(0.58–0.90)
S vs. W	S	17	0.585	(0.37–0.75)
WS vs. S	WS	23	0.005	(0.58–0.90)
WS vs. W	WS	20	0.099	(0.47–0.83)

The notation of choices in the treatments is: C clean patch, S spider mites, W whiteflies, WS spider mites and whiteflies

residence times were found for mixed-prey patches. No significant differences were found between treatments sharing the same initial prey patch (e.g. W–C, W–S and W–WS) suggesting that the patch leaving decisions of *A. swirskii* rely more on conditions in the actual patch than on the resource state of the alternative patch, which, according to the results from the preference experiment (see below), is likely to have been perceived from a distance. This would be in accordance with observations made for a specialist, an oligophagous and a polyphagous predatory mite that their responses to prey patches are caused by arrestment rather than attraction from a distance (Zhang and Sanderson 1992). However, the increased tendency to leave an initial single-prey patch in favour of an alternative patch harbouring prey (i.e. treatments W–WS, S–W, W–S, S–WS) compared to treatment WS–C may be seen as an attempt of *A. swirskii* to commute between patches that would allow it to obtain a mixed diet (Marques et al. 2015) and thus increase its fitness (Messelink et al. 2008).

Patch preference

Phytoseiids are eyeless and therefore rely on tactile, olfactory or mechano-sensory cues for detecting and recognizing their prey (Sabelis and Dicke 1985). The ability of predatory mites to use distant volatile resource information in their prey patch location or, together with local patch information, in their patch leaving decisions, is well-known, being described in several studies on both specialist (e.g. Maeda et al. 1998; Mayland et al. 2000; Sabelis and van de Baan

1983) and more generalist mite species (e.g. Dicke et al. 1989; Maeda and Takabayashi 2001; Shimoda 2010; Zhang and Sanderson 1992). Since the only cues available to *A. swirskii* in the present patch preference experiment was volatile cues, we conclude that this experiment confirms this ability in *A. swirskii*.

The experiment, which to our knowledge is the first on involving prey diversity in preference studies of generalist predator mites, demonstrated a preference of *A. swirskii* for patches with prey over uninfested patches and for mixed-prey patches over single-prey patches, although the latter was only significant when the choice involved single-prey patches with spider mites and merely tending to a difference when the single-prey species was whiteflies. The same distinct preference as observed for *A. swirskii* when offered spider mites (*T. urticae*) and thrips (*Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae)) (Xu and Enkegaard 2010), was not found here when the predatory mite had the choice between spider mites and whiteflies (S vs. W). A lack of preference was likewise found for *A. orientalis* (Ehara) when offered whiteflies (*Bemisia tabaci* (Gennadius)) and spider mites (*T. cinnabarinus* (Boisd.)) (Zhang et al. 2015). Our experimental set-up was void of both honeydew and spider mite webbing, substances previously shown to have an influence on the life history and behaviour of *A. swirskii* (Nomikou et al. 2003; van Houten et al. 2007; Messelink et al. 2010). Further investigations are needed to examine if the preference of the predatory mite between spider mites and whiteflies will change when infestations have progressed and the amount of these substances subsequently increased.

The preference for mixed-prey patches reflects that mixed-diets are more beneficiary to *A. swirskii* than uniform diets, as also evidenced by a significantly increased fecundity of *A. swirskii* when fed on a mixed spider mite and whitefly diet compared with single-species diets (S. Heydari, unpublished data). Messelink et al. (2008) likewise found higher juvenile survival and developmental rate of *A. swirskii* fed on a mix of whiteflies (*T. vaporariorum*) and thrips (*F. occidentalis*) than on either prey alone. Improved fitness as a result of mixed-diet feeding has also been noted for other generalist predatory mites (Munoz-Cardenas et al. 2014).

In conclusion, with its general preference for and lower tendency to leave mixed-prey patches compared to single-prey patches, *A. swirskii* has a patch-related behaviour tuned to exploiting the fitness gains of a mixed diet (Messelink et al. 2008; S. Heydari, unpublished data). Its patch-related behaviour is influenced by both local (i.e. the current patch) and distant information on patch resources (i.e. the nearby patches), with distant cues used in patch choosing and local cues in decisions on patch leaving. Our results suggest that also distant cues may be involved in patch leaving decisions, although further studies are needed to investigate if *A. swirskii* will practice commuting between single-prey patches (Marques et al. 2015) to obtain a mixed diet. In addition, more long-term studies under larger-scale greenhouse conditions are needed to evaluate the implications for practical biocontrol in greenhouse cultures with multiple pest infestations.

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