

Behavioural responses of two-spotted spider mites induced by predator-borne and prey-borne cues



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ABSTRACT

Applying predatory mites as biological control agents is a well established method against spider mites which are major pests worldwide. Although antipredator responses can influence the outcome of predator-prey interactions, we have limited information about what cues spider mites use to adjust their behavioural antipredator responses. We experimentally exposed two-spotted spider mites (*Tetranychus urticae*) to different predator-borne cues (using a specialist predator, *Phytoseiulus persimilis*, or a generalist predator, *Amblyseius swirskii*), conspecific prey-borne cues, or both, and measured locomotion and egg-laying activity. The reactions to predator species compared to each other manifested in reversed tendencies: spider mites increased their locomotion activity in the presence of *P. persimilis*, whereas they decreased it when exposed to *A. swirskii*. The strongest response was triggered by the presence of a killed conspecific: focal spider mites decreased their locomotion activity compared to the control group. Oviposition activity was not affected by either treatment. Our results point out that spider mites may change their behaviour in response to predators, and also to the presence of killed conspecifics, but these effects were not enhanced when both types of cues were present. The effect of social contacts among prey conspecifics on predator-induced behavioural defences is discussed.

1. Introduction

Animals are well adapted to gather information from their environment using various sensory modalities. Perceiving and adequately responding to cues on predators are especially important since the failure of predator recognition can result in immediate death (Lima and Dill, 1990). Besides visual and auditory cues, prey belonging to many invertebrate and vertebrate taxa evolved the ability to obtain information about predation threat via chemical cues (e.g. plankton: Lass and Spaak, 2003; mites: Grostal and Dicke, 1999; spiders: Lohrey et al., 2009; molluscs: Rochette et al., 1998; fish: Ferrari et al., 2005; amphibians: Hettyey et al., 2015; mammals: Apfelbach et al., 2005). Chemical information about the presence of enemies originate from two main sources: predator-borne (direct) and prey-borne (indirect) cues (Grostal and Dicke, 1999; Hettyey et al., 2015). Predator-borne cues include chemicals that dissipate from predators and their products, such as eggs, excreta, pheromones, tissue fragments or digestive body fluids, which may all be detected by prey (e.g. Dicke and Grostal, 2001; Hoffmeister and Roitberg, 1997). Moreover, excrements of predators can contain fragments originating from prey and provide information

about their feeding history (digestion-released cues; Hettyey et al., 2015). Finally, prey-borne cues include stress-, attack- and capture released cues that may originate from con- and heterospecific prey (Hettyey et al., 2015).

Prey exposed to predation threat usually exhibit a range of anti-predator behaviours that evolved to decrease the probability of predation, including lowered activity (e.g. Andersson et al., 1986), increased refuge use (Venzon et al., 2000; Faraji et al., 2001, 2002), avoidance of areas with predators (Pallini et al., 1999; Nomikou et al., 2003), increased vigilance (Sweitzer and Berger, 1992), egg retention (Montserrat et al., 2007), or altered patterns of habitat use (Lima and Dill, 1990). The ability to distinguish high-risk predators from less dangerous ones may provide additional benefits because failing to respond to the former could have irreversible consequences for prey (Chivers et al., 1996), while costs of responding to the latter may be spared. Therefore, the degree of these behaviours can depend on the level of risk posed by predators (e.g. Marko and Palmer, 1991; Vadas et al., 1994; Orrock et al., 2004; Walzer and Schausberger, 2009; Hettyey et al., 2011). Since prey are expected to use predator-borne cues to adjust the type and prey-borne cues to adjust the intensity of

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their response (Kishida and Nishimura, 2005; Teplitsky et al., 2005; Wilson et al., 2005; Hettyey et al., 2010), both cue types may be necessary to establish the full suite and intensity of induced defences (Grostal and Dicke, 1999; Schoeppner and Relyea, 2009; Hettyey et al., 2015).

Two-spotted spider mites (*Tetranychus urticae*) and their predatory mites offer an ideal model system to investigate how different levels of predation risk affect prey behaviour. The two-spotted spider mite is a well-known pest that infests commercial crop worldwide (Helle and Sabelis, 1985). Several predatory mite species are used against them as biological control agents, some of which are prey-specialists, while others are generalists (McMurtry et al., 2013). As a specialist, *Phytoseiulus persimilis* is most effective if prey abundance is high, while the generalist, *Amblyseius swirskii*, can also be used as a biological control agent preventively, because it can survive on alternative food (Chang and Kareiva, 1999; Symondson et al., 2002; Stiling and Cornelissen, 2005; Croft et al., 2004). Predatory mites are known to induce behavioural responses in spider mites: potential prey spend more time moving around and less time with feeding (Oku et al., 2004; Škaloudová et al., 2007), they show increased dispersal behaviour (Bernstein, 1984; Grostal and Dicke, 1999; Oku et al., 2003a, 2004; Otsuki and Yano, 2014), shifted oviposition site (Otsuki and Yano, 2017) and reduced egg-laying activity (Oku et al., 2004; Škaloudová et al., 2007; Choh et al., 2010), which could be especially beneficial against *P. persimilis* which prefers to feed on eggs (Blackwood et al., 2001).

In this paper, we investigated the effect of different predator- and prey-borne cues on the behaviour of the two spotted spider mite *T. urticae*. More specifically, we tested whether chemical cues of predators, either the specialist *P. persimilis* or the generalist *A. swirskii*, and prey-borne alarm cues interactively affect the locomotor and egg-laying activity of spider mites. Also, we examined how different prey-borne cues (visual and/or chemical) influenced the preys' responses to predation threat.

2. Materials and methods

2.1. Housing conditions and studied species

A two-spotted spider mite population (approx. 500 individuals) was established in September 2014 on common bean plants (*Phaseolus vulgaris*, L. cv. Sonesta) under controlled conditions (27 °C ± 0.5 °C, 60% humidity, L17:D7 cycle) at the Plant Protection Institute, Hungarian Academy of Sciences, Budapest, Hungary. We provided food *ad libitum* by transferring spider mite-infested bean leaves to clean, 3-week-old bean plants (2 beans/pot, 2–4 leaves/plant, not flowering) every week. Predator-naïve spider mite populations were reared for several generations and we collected mites for our experiments from this base population in March 2015. We used two commercially available predatory mite species (*P. persimilis* and *A. swirskii*, purchased from Árpád Biokontroll Ltd, Hungary), and kept them for 4 days without food in a fridge at 5 °C until the start of the experiment. Distributor fed *P. persimilis* with spider mites while *A. swirskii* with flour mites. All predators used in the experiments were females.

2.2. Experimental design

We conducted experiments in plastic cups (diameter 5 cm) at 27 °C ± 0.5 °C, 60% humidity and L17:D7 cycle on bean leaf discs (1.5 cm in diameter) on wet cotton (to prevent mites from leaving). To test how the cues of predatory mites or conspecifics influence the behaviour of spider mites, we treated leaf discs for 24 h in eight different ways prior to the allocation of focal individuals onto the discs. In the SP group (1), we placed ten spider mites onto leaf discs; in the SP- group (2), we also placed ten spider mites onto leaf discs, let them feed for 24 h and subsequently killed them with a needle and removed their

body before adding the focal individuals (see 2.3); in the SP+ group (3), we placed ten spider mites onto leaf discs, killed them with a needle and left their body on the leaf disc; in the PP group (4), we placed two *P. persimilis* predatory mites on the leaf disc; in the PP-SP group (5), we placed two *P. persimilis* predatory mites and ten spider mites on the disc; in the AS group (6), we placed two *A. swirskii* predatory mites on the leaf disc; in the AS-SP group (7), we placed two *A. swirskii* predatory mites and ten spider mites on the disc; in the C group (8), the leaf disc remained untreated (i.e. control group). We used five adult male and five adult female spider mites to prepare the treatments. Spider mites in the SP- and SP+ treatment groups were pierced once, which was sufficient to kill them. The body fluid of these individuals was allowed to flow onto leaf discs. After the 24 h-long treatments, we removed all live mites (both predatory and spider mites) as well as the bodies of killed individuals (except for the SP+ treatment) before placing focal mites onto the leaf discs. In SP, SP-, PP, PP-SP, AS, AS-SP groups we tested for potential responses to chemical cues, while in SP+ group we tested the effect of both visual and chemical cues. Each treatment was replicated twice on each of four consecutive days (resulting in a total of eight replicates per treatment).

2.3. Behavioural observations

Focal individuals consisted of six two-spotted spider mites (3 ♀, 3 ♂) that were placed onto each treated disc (henceforth referred to as the start of the experiment). We left them undisturbed for one hour to allow for habituation, and recorded their movement for another hour using a stereo microscope at ×10 magnification and a microscope camera attached to it. After this observation period, spider mites were allowed to lay eggs on the leaf discs for 94 h. 96 h after the start of the experiment, we removed mites from leaf discs and counted eggs. We analyzed mite behaviour based on video-recordings as follows: first, we layered a picture with a vertical and a horizontal line to the recording by which we divided the leaf disc into four equal parts (later referred to as grid). We analyzed locomotor activity and social behaviour of focal spider mites using the Observer XT software (version 11, Noldus Information Technology, Wageningen, Netherlands). We measured duration of (i) time spent moving, (ii) time spent standing, (iii) number of contacts with conspecifics, (iv) number of grid crosses and (v) number of grids explored. If a spider mite approached a conspecific to less than half a body length, we considered it a contact event, and used it as a measure of social behaviour. The simplest way of assessing social behaviour is to count the encounters (contacts) between individuals (e.g. Greene and Gordon, 2007; Whitehead, 2008). The other four variables (i, ii, iv, v) characterized the general activity of spider mites (e.g. Le Goff et al., 2012; Hackl and Schausberger, 2014). As the video-recordings slightly differed in their total duration (min-max: 59.083–62.7), we calculated proportions of time spent with various behaviours by dividing each measure by the length of the recording (in min). We could not assess potential differences in the behaviour of males and females because the resolution of the video-recordings did not allow for identifying sex. Ten out of 384 focal individuals died during the experiments.

2.4. Statistical analyses

As the observed behavioural traits were coded with each spider mite individually, we calculated the mean of each variable per leaf disc and used these values for further analyses. Since our measures of locomotor activity (rate of moving, rate of standing, rate of grid crosses and rate of grids explored) were highly correlated (all $P < 0.01$, all $r_s > 0.723$), we subjected them to a Principal Component Analysis. The first principal component explained 82% of the total variance, so we used PC1 component scores as a measure of general activity in further analyses. Rate of moving, rate of grid crosses and rate of grids explored loaded positively on the first component (rate of moving: 0.940, rate of grid

crosses: 0.875, rate of grids explored: 0.897), while rate of standing loaded negatively on it (-0.939). Variation between the six individuals within leaf discs was substantial (min-max, median): rate of moving: 0.001–0.065 (0.016), rate of standing: 0.001–0.064 (0.016), rate of grid crosses: 0–4.58 (0.061), rate of grids explored: 0–0.001 (0.0002) and rate of contacts: 0–0.111 (0.012). To enhance normality of model residuals and homogeneity of variances, we performed box-cox transformation on the rate of contacts variable.

We used linear mixed-effect models to investigate whether predator-borne and prey-borne chemical cues affected spider mites' locomotor activity (PC1), rate of contacts and number of eggs laid. Into each model, we included the chemical cues on predators (three levels: absence of predators, *A. swirskii* predator, *P. persimilis* predator), chemical cues on killed conspecifics (two levels: presence or absence) and their interaction as explanatory variables. We also applied linear mixed-effect models to test if the presence of chemical cues originating from live or killed conspecifics, or both chemical and visual cues on killed conspecifics influenced the above responses of focal individuals. We added the day of trial as a random factor to all models. We also entered locomotor activity as an explanatory variable into the analyses on the rate of contacts to control for the activity-related changes in the frequency of contacts between mites.

We used F-tests to evaluate significance of the explanatory variables and a stepwise backward elimination procedure to find the best-fitting models. We applied Tukey HSD post-hoc tests to explore differences between treatment groups. We checked whether the requirements of fitted models were met using plot-diagnosis. Statistical analyses were carried out in R 3.2.2 (R Core Team, 2015) using the car (Fox and Weisberg, 2011), lme4 (Bates et al., 2015) and lsmeans R packages (Lenth, 2016).

3. Results

3.1. Behavioural and oviposition responses to predator-borne and prey-borne cues

Exposure to predator cues had a significant effect on the spider mites' locomotion activity ($F_{1,2} = 13.20, P < 0.01$). Increased activity was observed when spider mites were released on specialist predator-exposed (*P. persimilis*) leaf discs as compared to generalist predator-exposed (*A. swirskii*) leaf discs or to control leaf discs (Fig. 1). In contrast, spider mite activity was not affected by cues originating from killed conspecifics ($F_{1,1} = 1.89, P = 0.17$). The interaction between predator-borne cues and cues originating from killed conspecifics was non-significant ($F_{1,2} = 2.22, P = 0.33$).

The rate of contacts was positively related to activity ($\beta = 0.01$; SE = 0.001; $F_{1,1} = 46.66, P < 0.01$), however it was not affected by the presence of predator-borne cues ($F_{1,2} = 0.71, P = 0.70$), by cues originating from killed conspecifics ($F_{1,1} = 0.40, P = 0.53$), or their interaction ($F_{1,2} = 2.88, P = 0.24$).

The number of eggs laid was not associated with the presence of predator-borne cues ($F_{1,2} = 4.23, P = 0.12$, Fig. 2), by cues originating from killed conspecifics ($F_{1,1} = 0.16, P = 0.68$), or their interaction ($F_{1,2} = 0.09, P = 0.95$).

3.2. Behavioural and oviposition responses to chemical and visual cues on the presence of conspecifics

Cues originating from conspecifics had a significant effect on spider mite activity ($F_{1,3} = 17.03, P < 0.01$): activity was lower in the presence of killed conspecifics and when only their chemical cues were present than on clean leaves (Fig. 3). None of the other comparisons was significant.

The rate of contacts was not affected by cues originating from conspecifics ($F_{1,3} = 4.60, P = 0.20$) while it was affected by locomotion activity ($F_{1,1} = 20.94, P < 0.01$). The number of eggs laid was not

significantly affected by cues originating from conspecifics ($F_{1,3} = 3.10, P = 0.38$, Fig. 4).

4. Discussion

In this study, we demonstrated that spider mites can show different behavioural responses to chemical cues originating from specialist and generalist predators: prey responded to the presence of cues on a specialist predator with increased activity as compared to the presence of chemical cues on a generalist predator or in the absence of cues on a predator threat. When investigating the impact of different prey-borne cues, we found that spider mites decreased their activity in the presence of killed conspecifics (i.e. both visual and chemical cues) and in the presence of only chemical cues on killed conspecifics as compared to the control group. We found no effect of predator- or prey-borne chemical cues on the number of eggs focal spider mites laid or on the rate of contacts between spider mites.

Our finding that in the presence of chemical cues on the specialist predator *P. persimilis* spider mites had increased locomotor activity is in line with previous findings: reported significantly increased walking activity in spider mites exposed to cues in the presence of *P. persimilis*. In addition, Bernstein (1984) found that *T. urticae* leave the plant in the presence of *P. persimilis*. Since *P. persimilis* find their prey via volatiles emitted by the spider mite-infested plant (Dicke, 1986; Takabayashi and Dicke, 1993; Dicke et al., 1998; Kant et al., 2004), it could be beneficial for spider mites to quit feeding and migrate to a new plant. Our results support this as we found higher activity in the presence of *P. persimilis* chemical cues but not in the presence of *A. swirskii* chemical cues. Thaler and Griffin (2008) also found similar evidence for the non-consumptive effect of predators: *Manduca sexta* caterpillars spent less time feeding in the presence of predators than in their absence (Kats and Dill, 1998). Our experimental setup did not allow spider mites to leave leaf discs, but their drive to move away from the predator may have manifested in the observed elevated movement activity. We also found that the generalist *A. swirskii* did not cause a similar response in activity as the specialist. A possible explanation for the discrepancy between responses to the two predators could be that *P. persimilis* has been used against spider mites since the 1960s, while *A. swirskii* was introduced into the market only in 2005. Also, as in other predator-prey systems (e.g., Peckarsky, 1996; Teplitsky et al., 2004; Hettyey et al., 2011), the stronger response to *P. persimilis* may have been due to it being a more voracious predator of spider mites than *A. swirskii*. Therefore, it appears that spider mites have evolved responses against *P. persimilis*, but not, or not yet, to *A. swirskii*. This interpretation is in line with results of Dias et al. (2016) who also found stronger induced antipredator defences in spider mites in response to cues of a dangerous predator than to cues of a harmless predator. In addition, we propose that further research is needed to investigate potential sex-dependent differences in spider mites' antipredator behaviour, especially because some previous studies observed that predators induced more intense antipredator behaviours in males (Abrahams and Dill, 1989; Ball and Baker, 1996), while in other cases females responded more intensely (e.g. Williams et al., 2001; Magurran and Seghers, 1994).

Animals exposed to cues from injured or killed conspecifics have often been shown to display antipredator behaviours (Pijanowska, 1997; Chivers et al., 1996; Janssen et al., 1997). We observed the strongest decrease in spider mite activity when they were exposed to the presence of killed conspecifics and a similarly strong response to only the chemical cues originating from killed conspecifics. Killed conspecifics may emit capture-released alarm signals before they are killed that make other conspecifics aware of danger (e.g. Smith, 1992; Bowers et al., 1972; Teerling et al., 1993). In contrast, if the potential threat is not recognizable, an adaptive strategy might be to spend more time inactive (e.g. Wudkevich et al., 1997; Hazlett, 1994; Smith, 1989). Oku et al. (2003b) found that *Tetranychus kanzawai* females took refuge in the webbing at a higher probability when they were exposed to

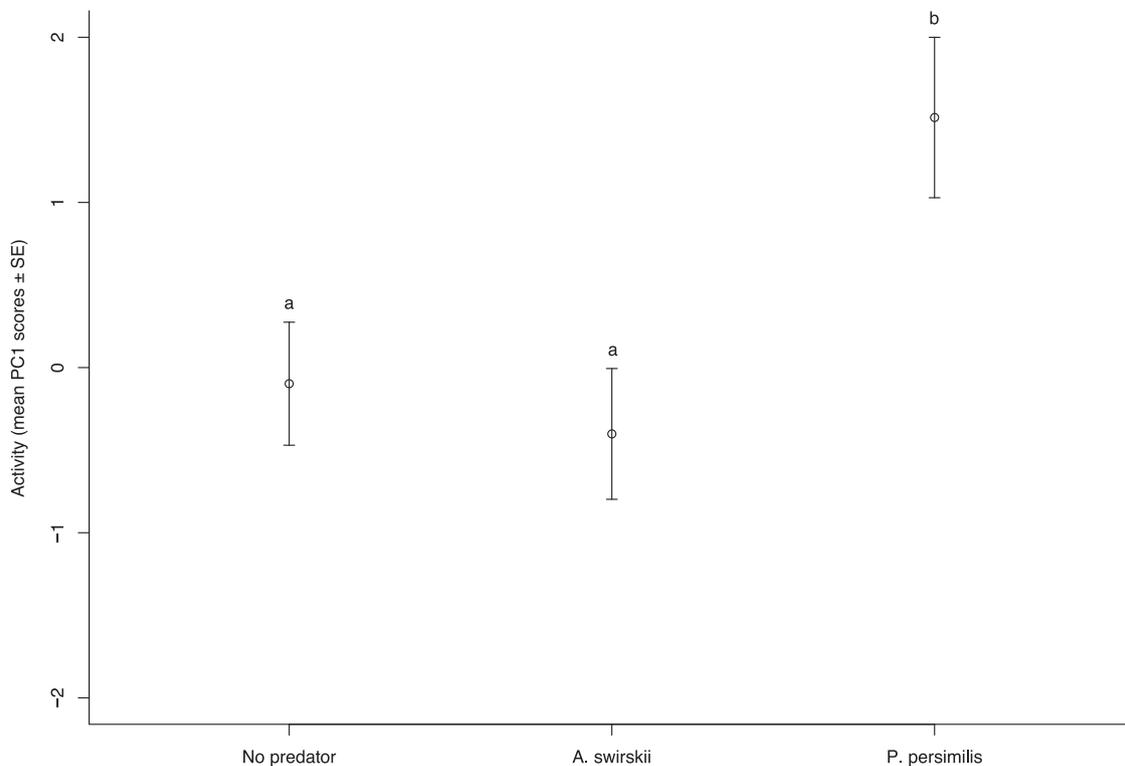


Fig. 1. Effect of predator- borne cues on spider mites' locomotor activity (mean \pm SE). Activity was calculated using Principal Component Analysis (for further details see the text). The higher value of PC1 score describes more activity. 'No predator' group involved control and chemical cues on killed spider mites groups. Number of replicates were 16 per groups. Different letters are significantly different based on Tukey's honestly significant difference (HSD, $P < 0.05$).

injured conspecifics than to intact conspecifics. [Grostal and Dicke \(1999\)](#) demonstrated that spider mites (*T. urticae*) avoided injured conspecific-exposed leaves. In addition, we observed somewhat lower activity in spider mites that were exposed to cues of feeding

conspecifics, but this effect was not significant. Cues of feeding conspecifics can be expected to affect activity, because silk-covered leaf discs may provide shelters against certain predators ([Le Goff et al., 2012](#)), and because the presence of silk may indicate the presence

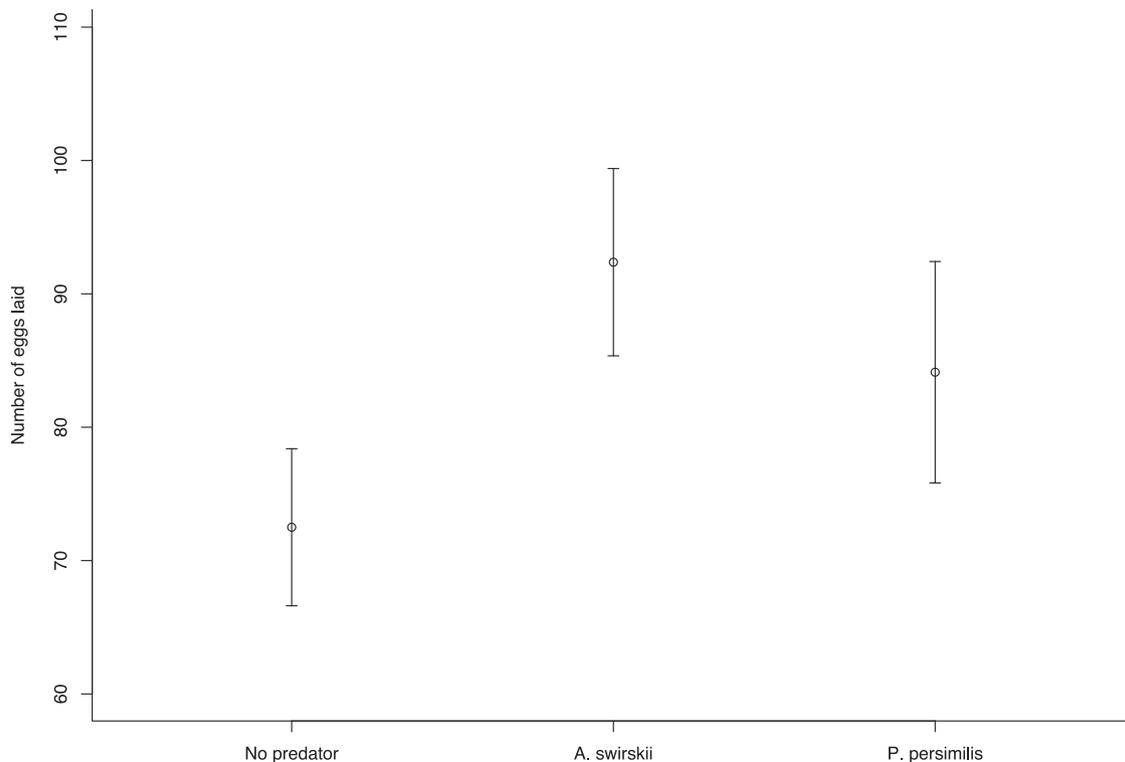


Fig. 2. Effect of predator- borne cues on spider mites' oviposition activity (mean \pm SE). 'No predator' group involved control and SP- groups. Number of replicated were 16 per groups. The number of eggs laid was not affected by the presence of predator- borne cues.

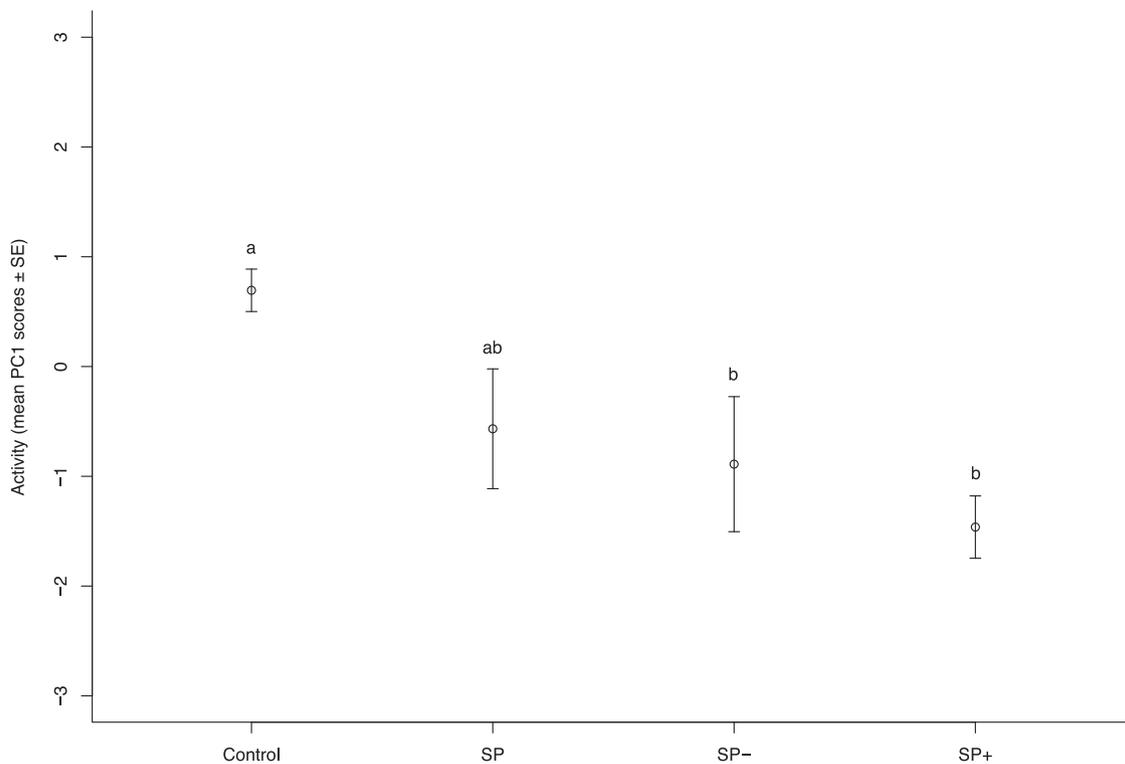


Fig. 3. Effect of prey-borne cues on spider mites' locomotor activity (mean \pm SE). The higher value of PC1 represents more active spider mites. Abbreviations: C: control, SP: chemical cue of living spider mites, SP-: chemical cue of killed spider mites, SP+: visual and chemical cue of killed spider mites. Number of replicates were 8 per treatments. Different letters are significantly different based on Tukey's honestly significant difference (HSD, $P < 0.05$).

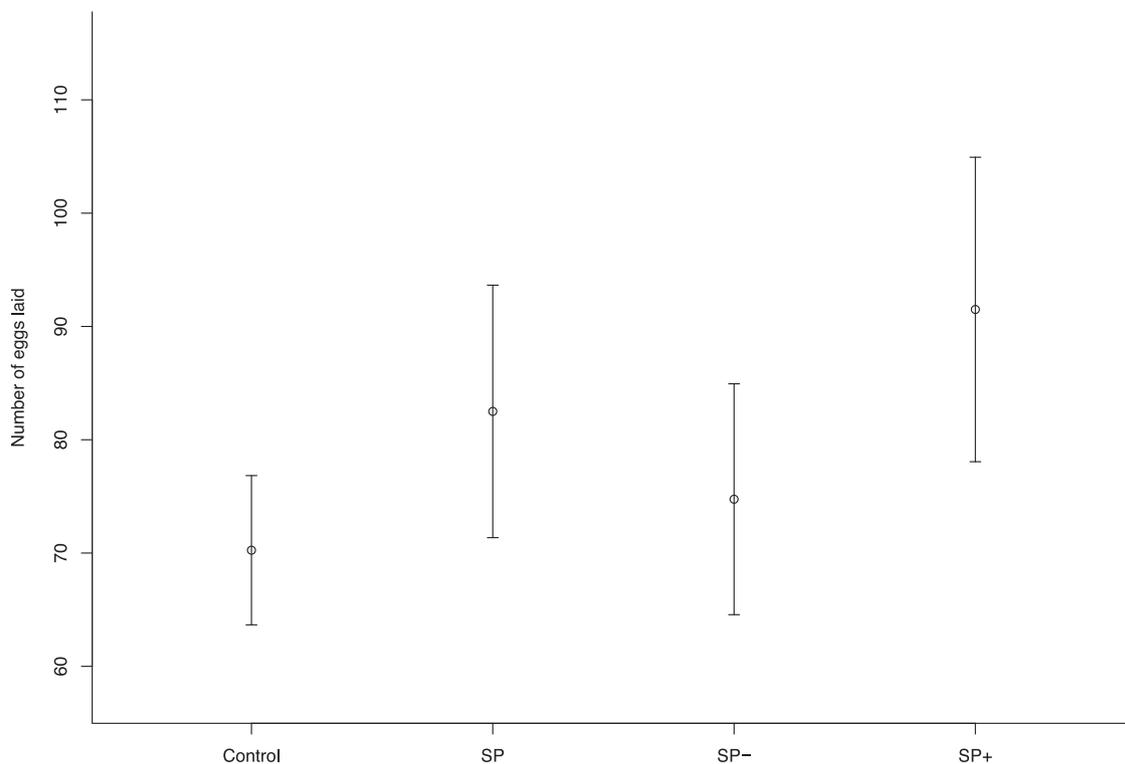


Fig. 4. Effect of prey-borne cues on spider mites' oviposition activity (mean \pm SE). Abbreviations: C: control, SP: chemical cue of living spider mites, SP-: chemical cue of killed spider mites, SP+: visual and chemical cue of killed spider mites. Number of replicates were 8 per treatments. The number of eggs laid was not affected by the presence of prey-borne cues.

of conspecifics and, thereby, lowered per capita predation risk. Consequently, instead of producing the silk webbing immediately as spider mites usually do when introduced to a new environment (Bancroft and Margolies, 1996), they could invest into other activities, such as feeding

or laying eggs.

There is an evolutionary arms race between predators and prey in which detection and evasion essentially affect the outcome (Dawkins and Krebs, 1979). Spider mites use vibration, volatile and tactile

chemosensory cues to evaluate predation risk (Kats and Dill, 1998; Dicke and Grostal, 2001). For instance, Azandémè-Hounmalon et al. (2016) documented avoidance behaviour in *Tetranychus evansi* in the presence of predatory *Phytoseiulus longipes* in response to visual, vibratory and olfactory cues that spider mites used independently or simultaneously. Studies performed on other taxa also indicated that individuals are better able to assess predation risk when they are exposed to visual and chemical cues (e.g. Chivers et al., 2001; Mathis and Vincent, 2000). Surprisingly, we found that locomotor activity was not affected interactively by chemical cues on predators and conspecifics, this latter affected mites' behaviour only in the absence of predator cues. Due to the foraging mode of the two predators, we expected a larger increase in locomotor activity in the presence of cues on the presence of the specialist predator (*P. persimilis*) and of conspecifics compared to the presence of cues of the generalist predator (*A. swirskii*). However, further studies are needed to clarify the origin and the sensory-physiological pathways of chemical cues that induce behavioural responses to predation threat in *T. urticae*.

It is known that *T. urticae* display various forms of social behaviour such as aggregation (Le Goff et al., 2009, 2010), or the construction of a common web (Saito, 1983; Clotuche et al., 2009; Le Goff et al., 2012). Protection from predators is one of the advantages of living in a group, with benefits such as dilution of predation, group vigilance and the confusion effect (e.g. Hamilton, 1971; Lack, 1954; Landeau and Terborgh, 1986). Several studies investigated changed behaviour including increased aggregations in the presence of a potential predator (e.g. Reimer and Tedengren, 1997; Turchin and Kareiva, 1989). In addition, Berec et al. (2016) found that tadpoles decreased their swimming activity when cues of predators were present, but only when tadpoles did not have contact to conspecifics. Van Buskirk et al. (2011) demonstrated that prey density effects on the expression of defensive behaviour in *Rana temporaria* tadpoles, because they increased their activity at a high conspecific density. Also, in bird species group size have an important role in predation avoidance (e.g. Beauchamp, 2004). However, in our study, spider mites did not show systematic, treatment-dependent alterations in the rate of contacts. Nonetheless, future, more detailed studies may reveal changes in the social behaviour of spider mites in response to predator- or prey-borne cues, especially so in larger experimental populations.

We found that predator-borne or prey-borne cues did not have any effect on the number of eggs laid by spider mites. This finding partly contradicts previous studies in which spider mites were found to produce fewer eggs as a response to predator cues (Oku et al., 2004; Škaloudová et al., 2007; Choh et al., 2010). Moreover, Dias et al. (2016) showed that *Tetranychus evansi* females laid fewer eggs in the presence of cues of a dangerous predator (*Phytoseiulus longipes*) than in the absence of predators, or in the presence of a harmless predator (*Phytoseiulus macropilis*). Another study compared egg retention of spider mites in response to *P. persimilis* and *A. swirskii* predators but did not reveal any differences (Yazdi et al., 2015). It is possible that the lack of induced changes in oviposition rates in our study is due to the experimental design, because we measured the number of eggs laid during 4 days after first exposure to various cues. Although Kriesch and Dicke (1997) found that spider mites responded to 4-day old predator kairomones, observed differences in the number of eggs laid only on the first day, suggesting – similarly to our study – that chemical cues on predators are likely to evaporate quickly from the surface of leaves. We suggest that further investigations related to the specificity and intensity of phenotypic responses to different predators could help better understand the non-consumptive effects of predators and may contribute to obtaining more precise estimates of realized predation rates in this important model system.

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