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The presence of webbing affects the oviposition rate of two-spotted spider mites, *Tetranychus urticae* (Acari: Tetranychidae)

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Abstract Several species of tetranychid mites including *Tetranychus urticae* Koch (Acari: Tetranychidae) construct complicated three-dimensional webs on plant leaves. These webs provide protection against biotic and abiotic stress. As producing web is likely to entail a cost, mites that arrive on a leaf with web are expected to refrain from producing it, because they will gain the benefit of protection from the existing web. Mites that produce less web may then allocate resources that are not spent on web construction to other fitness-enhancing activities, such as laying eggs. To test this, the oviposition rate of *T. urticae* adult females was examined on leaves with web. As a control, we used leaves where the web had been removed, hence both types of leaves had been exposed to conspecifics previously and were thus damaged. On leaves with web, the oviposition rate of *T. urticae* females was higher than on leaves where the web had been removed. Therefore, the presence of web constructed by conspecifics enhanced the oviposition rate of *T. urticae* females. This provides indirect evidence that mites use the web constructed by conspecifics and thereby save resources that can be allocated to other traits that enhance reproductive success.

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Introduction

Living in a group may be advantageous for organisms (Allee et al. 1949; Wertheim et al. 2005). For example, it may enhance the growth rate of populations (e.g. Denno and Benrey 1997), or reduce an individual's risk of predation (e.g. Watt et al. 1997; Viscido and Wethey 2002). However, living in groups may also entail costs, as it enhances intraspecific competition (e.g. Despland and Le Huu 2007) as well as the opportunity for cannibalism.

Tetranychid mites including *Tetranychus urticae* Koch (Acari: Tetranychidae) often live in a group on their host plants (e.g. Takafuji and Kamibayashi 1984; Gotoh 1997; Gotoh et al. 2007). They construct a complicated three-dimensional web over the leaf surface of their host plant (Saito 1983). The webs of tetranychid mites function as a place for excretion (Saito 1983; Oku 2008), as protection against adverse climate conditions, such as wind or rain (Davis 1952), and against predators (McMurtry et al. 1970; Oku et al. 2003, 2004). Thus, living in a group may be beneficial for spider mites because the web becomes denser. However, it may also entail costs, such as increased intraspecific competition. In addition, because web is composed mainly of proteins (Hazan et al. 1975), it is expected that spider mites allocate considerable resources to producing web.

When *T. urticae* founds a new colony, it first constructs a web over the leaf undersurface (Saito 1979). Thus, individuals that arrive later may benefit from the protection conferred by that web, while bypassing the potential costs associated with web production. If this is true, the individuals arriving on a leaf containing a web are expected to allocate the resources they would use to produce web to other fitness-enhancing activities. In this study, we examined the effects of the presence of web constructed by conspecifics on the oviposition rate of *T. urticae* females and discuss the results in the light of the potential benefits and costs associated to the presence of a conspecific web. Since the effect of the web, for example the protection it confers to spider mite eggs, varies with the host plant (Magalhães et al. 2005), we performed the experiment on two different host plants.

Materials and methods

Mite cultures

Host plant: bean. *Tetranychus urticae* was reared on Lima bean plants (*Phaseolus lunatus* L. cv. Sieva) in a greenhouse (25 ± 5°C, 50–70% relative humidity, L16:D8) at Wageningen University in large numbers (>10,000). The mites originated from a mass-rearing at a biological control company and have been reared continuously on Lima bean since then. *Tetranychus urticae* was often reared at relatively high densities. Since the performance of *T. urticae* females is affected by their density during development (Oku et al. 2002), one generation before being used in experiments the spider mites were reared separately from the stock culture. To mitigate density effects, adult females, randomly selected from the stock culture, were transferred to *P. lunatus* leaves (10 mites per leaf) placed on water-saturated cotton wool and allowed to oviposit under laboratory conditions (25 ± 5°C, 50–70% relative humidity, L16:D8). Individuals of the next generation were used for the following experiments.

Host plant: cucumber. Cucumber plants were sown once per week and cultured in an herbivore-free room under controlled conditions (25°C). Cucumber seeds (variety Ventura) were provided by Rijk Zwaan Nederland B.V. (De Lier, Netherlands). *Tetranychus urticae* was reared in large numbers (>10,000) on cucumber plants (approximately 4 weeks old, provided twice a week) under controlled conditions (25°C) in a separate room. *Tetranychus urticae* was originally collected from a cucumber greenhouse (variety: Ventura) in Pijnacker, The Netherlands, in May 1994 and kept on that same variety in a climate chamber at the University of Amsterdam.

Effects of the presence of web on the oviposition rate of *Tetranychus urticae*

Bean: To examine whether the presence of web affects the oviposition rate of *T. urticae* females, 70 bean leaf squares (20 × 20 mm) were cut and placed on water-saturated cotton wool. Ten newly emerged *T. urticae* females were transferred to each of 70 bean leaf squares, and allowed to construct a web on the leaf surface under laboratory conditions. Since spider mites do not lay eggs within 24 h after adult emergence at 25°C (Furuichi et al. 2005), the web remained free of *T. urticae* eggs. The method described in Furuichi et al. (2005) was followed to obtain newly emerged *T. urticae* females. After 24 h, the *T. urticae* females were removed from the leaf squares. Then, the web was removed from half of leaf squares by using a fine brush ('without web', $n = 35$), and the webs of the rest of leaf squares remained intact ('with web', $n = 35$). One *T. urticae* adult female (3-day-old since the last moult), which had been starved for one day, was introduced onto each of the leaf squares. After 6 and 24 h since introduction, the number of eggs laid by the *T. urticae* females was counted on each leaf square, and compared between treatments using a one-way ANOVA test.

Cucumber: 10 females were allowed to oviposit on each of 50 cucumber leaf discs (∅ 15 mm) and produce web during 48 h. They were subsequently removed and their eggs punctured with a fine needle. The web was then removed in half of those leaf discs with a fine brush and one female spider mite (10–12 days old since emergence from the egg) per leaf disc was introduced. We counted the eggs laid by each female during 5 days or until the female died or drowned in the water. Data were analysed with an ANOVA using SPSS, with presence of web as a fixed factor and day as a covariable. To test whether differences in oviposition rate remained significant throughout the experiment, we subsequently analysed differences in oviposition rate between leaf discs with and without web for each day separately.

Results and discussion

On Lima bean, the oviposition rate of *T. urticae* females on leaf squares where web had been constructed by conspecifics during 24 h, was significantly different after 24 h ($F_{1,68} = 4.557$, $P = 0.036$; Fig. 1). This result indicates that the presence of a web enhances the oviposition rate of *T. urticae* females on bean plant. However, after 6 h, a significant difference was not yet found ($F_{1,68} = 1.247$, $P = 0.268$). Adult females of *T. urticae* produce eggs from resources ingested within the last 24 h (e.g. Yano et al. 1998). The *T. urticae* females used in this experiment were starved for one day to eliminate the effect of feeding prior to the experiment. Therefore, 6 h is probably too short for *T. urticae* females to gain enough energy to produce eggs.

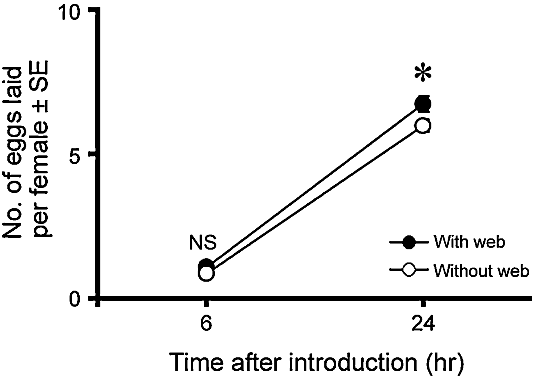

Fig. 1 Effect of the presence of webs on the oviposition rate of *Tetranychus urticae* females on bean plants. *Vertical bars* indicate standard error of the mean. $*P < 0.05$ (ANOVA test)

On cucumber leaf discs, a significant effect of the presence of web on the oviposition rate of *T. urticae* females was found (ANOVA, $F_{1,193} = 4.39$, $P = 0.037$; Fig. 2). The oviposition rate decreased significantly with time, as indicated by the significance of the covariable ($F_{1,193} = 31{,}84$, $P < 0.0001$). This is probably a result of decreased quality of the leaf disc. When analysing each day separately, a significant difference in oviposition rate between treatments was found on the first day only ($F_{1,47} = 5.83$, $P = 0.0197$, for the first day, in all other days $P > 0.35$). This result indicates that the oviposition rate of *T. urticae* in cucumber is also higher in the presence of web, albeit for a limited time period.

When *T. urticae* females found a new colony, they first construct a web over the leaf surface and subsequently start feeding on the plant (Saito 1979). A web previously constructed by conspecifics can be used by another female arriving later at the same patch. This allows the second female to save resources that can be spent on feeding and egg production. As a result, *T. urticae* females arriving on a patch with web can lay more eggs than females arriving at a place without web. However, 48 h after the introduction of individuals on leaves with web, the benefit of web presence was no longer evident. This may be because in subsequent days, web was reconstructed on the leaves without web,

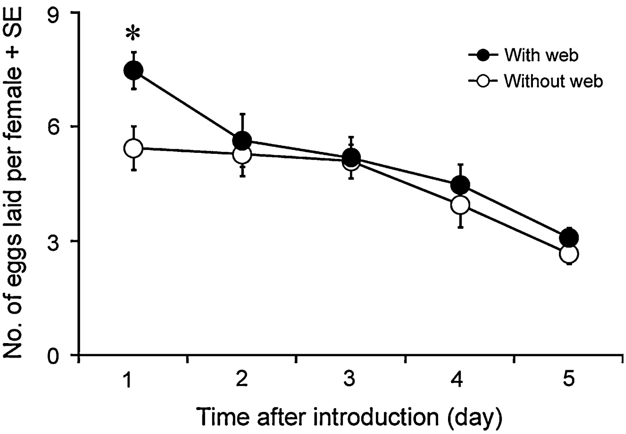

Fig. 2 Effect of the presence of web on the oviposition rate of *Tetranychus urticae* females on cucumber plants. *Vertical bars* indicate standard error of the mean. $*P < 0.05$ (ANOVA test for each day)

thereby reducing differences between treatments. Whether this difference in oviposition rate in patches with and without web will affect the growth rate of spider mites will depend on several factors, namely on the age of spider mites when arriving on new leaves, as differences in oviposition rate are more relevant for the growth rate at early ages (Sabelis 1991). In any case, these differences provide indirect evidence that producing web consumes resources that can otherwise be allocated to other traits such as reproduction.

Using web produced by conspecifics implies living in a group. The web produced by tetranychid mites protects them from several predators (Gerson 1985; Trichilo and Leigh 1986; Mori et al. 1999; Oku et al. 2003). Denser spider mite colonies of spider mites are expected to produce denser webs, conferring better protection from predators. However, denser mite colonies are more easily found by predatory mites (e.g. Maeda and Takabayashi 2001; Gols et al. 2003), and they are expected to entail more intraspecific competition. Hence, both the costs and the benefits of living in a group are expected to increase with the density of conspecifics.

The spider mite web may be exploited by other species, such as specialist predators of the spider mites, or competitors, which use the web as a protection against their own natural enemies (e.g. Roda et al. 2000; Magalhães et al. 2007). These species do not produce the web that they use, hence they will not be affected by the benefit of not producing web. Hence, our results lead to the prediction that the relative advantage of spider mites over their competitors will increase with the density of conspecifics that produce web. After some time, however, this initial advantage will wane.

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