

Comparison of thread-cutting behavior in three specialist predatory mites to cope with complex webs of *Tetranychus* spider mites

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Abstract Anti-predator defenses provided by complex webs of *Tetranychus* mites can severely impede the performance of generalist predatory mites, whereas this may not be true for specialist predatory mites. Although some specialist predatory mites have developed morphological protection to reduce the adverse effects of complex webs, little is known about their behavioral abilities to cope with the webs. In this study, we compared thread-cutting behavior of three specialist predatory mites, *Phytoseiulus persimilis*, *Neoseiulus womersleyi* and *N. californicus*, exhibited inside the complex web of *T. urticae*. No major difference was observed among them in the basic pattern of this behavior, using chelicerae and palps, and in the number of silken threads severed while moving inside the web. These results and observations suggest that each predator species cut many sticky silken threads to move inside the complex web without suffering from serious obstruction.

Keywords Spider mite · Complex web · Defense · Predatory mite · Specialist · Counteradaptation

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Introduction

Producing webs on host plants is one of the principal characteristics of many plant-inhabiting spider mites. A typical example is the dense, complicated, 3-dimensional, sticky webs (called “complex webs”) produced by genus *Tetranychus* spider mites (see Fig. 1.4.4.7 in Saito 1985). Complex webs have various possible functions, one of which is defense against predators (Gerson 1985; Saito 1985). They can repel predators (McMurtry and Johnson 1966; Takafuji and Chant 1976), inhibit predators’ free movement (Putnam 1962; McMurtry et al. 1970; Trichilo and Leigh 1986), or entrap predators, which frequently results in the death of the predator (McMurtry and Scriven 1964; Trichilo and Leigh 1986; Osakabe 1988). Given that adult females and immature stages (e.g., larvae, nymphs or teleiochrysalises) of spider mites reside inside the webbed areas, complex webs protect them against predatory mites (Putnam 1962; Oku et al. 2003, 2004).

It is empirically considered that predators experience difficulty in avoiding contact with the sticky silken threads when they enter and move inside complex webs (Sabelis and Bakker 1992). However, the degree of the adverse effects of complex webs on their performance may depend on the type of predator. For example, as suggested by the aforementioned reports, anti-predator defenses provided by the complex webs can severely impede the performance of many generalist predatory mites. However, this may not be the case for specialist predators (Sabelis and Bakker 1992; McMurtry and Croft 1997). For instance, some specialist predatory mites and insects that chiefly thrive on *Tetranychus* mites can readily enter and move within complex webs without suffering serious obstruction by sticky silken threads (Putnam 1955; Gilstrap and Oatman 1976; McMurtry and Croft 1997; Shimoda et al. 1997). In specialist predatory mites, such as *Phytoseiulus persimilis*, *Neoseiulus californicus* and *N. womersleyi*, morphological protection (e.g., long dorsal setae) may reduce the dangers of contact with sticky silken threads during their movements inside complex webs (Sabelis and Bakker 1992).

Specialist predatory mites and insects may behaviorally reduce the adverse effects of the sticky silken threads when they move inside complex webs. For example, we have reported that adult staphylinid predators of *Oligota kashmirica benefica* cut many silken threads (provisionally called “thread-cutting behavior” in this paper) during their movements within the complex webs of *Tetranychus urticae* (Shimoda et al. 1997). Similar thread-cutting behavior using a grasping organ normally used for capturing and eating prey (i.e., chelicerae) can be seen in several specialist predatory mites, such as *P. persimilis*, *N. womersleyi* and *N. californicus*, in complex webs of *T. urticae* (Shimoda et al. 2003). On the other hand, different types of thread-cutting behavior may be expressed in predatory mites when they face different types of spider-mite webs: Montserrat et al. (2008) reported that *N. californicus* use their first pair of legs when ripping and destroying the walls of web nests constructed by the persea mite *Oligonychus perseae*. This argument prompts an interesting question as to what type of thread-cutting behavior is adopted by *N. californicus* and other specialist predatory mites to cope with the complex webs produced by *Tetranychus* mites. To date, however, little attention has been paid to the subject, regardless of a large number of behavioral observations on their activities in complex webs (McMurtry and Croft 1997). This may be largely due to the difficulty of observing the very fine, transparent silken threads (0.03–0.06 μm in diameter) of the complex webs, even with the use of a binocular microscope (Gerson 1979).

The main purpose in this paper is to describe the thread-cutting behavior of three specialist predatory mites (*N. californicus*, *N. womersleyi* and *P. persimilis*) expressed when they move in the complex web of *T. urticae*. In this study, we first described suitable conditions for observing both fine silken threads and thread-cutting behavior. We then

investigated the following two subjects: (1) how each predator breaks silken threads, and (2) how many silken threads are severed by each predator while moving inside the web (provisionally referred to as “efficiency of thread-cutting behavior”). In this paper, we will show that each predator species can cut many silken threads with similar thread-cutting behavior (using chelicerae and palps only), which contributes significantly to their successful movement inside the web.

Materials and methods

Plants and mites

Kidney bean plants (*Phaseolus vulgaris*, cv. Nagauzurumame) were cultivated individually in clay pots (9 cm in diameter, 7 cm in depth) in a climate-controlled room ($20 \pm 1^\circ\text{C}$, $60 \pm 20\%$ r.h. and 16L:8D photoperiod). Young kidney bean plants, 2–3 weeks after germination, were used for rearing the prey and predators. Kudzu vine plants [*Pueraria lobata* (Wild)] were used for behavioral observation experiments. The kudzu leaves were collected from a field at the National Agricultural Research Center, Ibaraki Prefecture, Japan. The following experiments were conducted from August to November 2001.

Neoseiulus womersleyi and *N. californicus* were obtained from Dr. N. Hinomoto, of the National Institute of Agrobiological Sciences, Tsukuba, Ibaraki Prefecture, Japan, in 1999. *P. persimilis* was obtained from a commercial source (Koppert BV, The Netherlands) in 1998. Each predator had been reared for several years on *T. urticae* on kidney bean leaves in a climate room ($20 \pm 1^\circ\text{C}$, $60 \pm 20\%$ r h. and 16L:8D photoperiod). Adult females of each predator species were individually placed in plastic sampling tubes (2.0 ml), containing a small piece of moist filter paper, in a laboratory ($25 \pm 1^\circ\text{C}$) several hours prior to the experiment. Three- to five-day-old individuals after the final molting followed by mating in each predator species were used in this study.

Experimental procedure

A piece of kudzu vine leaf (5×5 cm), hereinafter called a “leaf quadrat,” was placed on water-soaked cotton wool in a petri dish (9 cm in diameter, 1.7 cm in depth). Thirty *T. urticae* adult females were introduced onto each leaf quadrat using a fine paintbrush and then maintained for 2 days in a climate-controlled room ($25 \pm 1^\circ\text{C}$ and 16L:8D photoperiod). Following this treatment, the density of spider mites on each leaf quadrat was ascertained (30 adult females and ca. 600 eggs per leaf quadrat) using a binocular microscope (Nikon SMZ-2T, magnification: 8–80 \times) under (sub-) vertical light from a cold light source (Hoya Schott, PL-075 W). It was difficult to observe the silken threads clearly under these conditions, since both the surface of the leaf quadrat and the very fine threads reflected light to a similar extent. However, we found suitable conditions for viewing the threads illuminated brightly against a dark background by changing the angle of the light to 5–25 $^\circ$ from the horizontal plane.

Under these suitable observation conditions, we introduced one adult female of a predator species to each leaf quadrat using a fine paintbrush. After the settlement of each predator (ca. 30–60 s. after the introduction), we started observing the behavioral activities inside and outside the web for 10 min in a laboratory ($25 \pm 1^\circ\text{C}$). We recorded the total time of each behavior inside or outside the complex web according to the following three categories (Fig. 1): (1) moving inside the web: moving forward or backward inside the

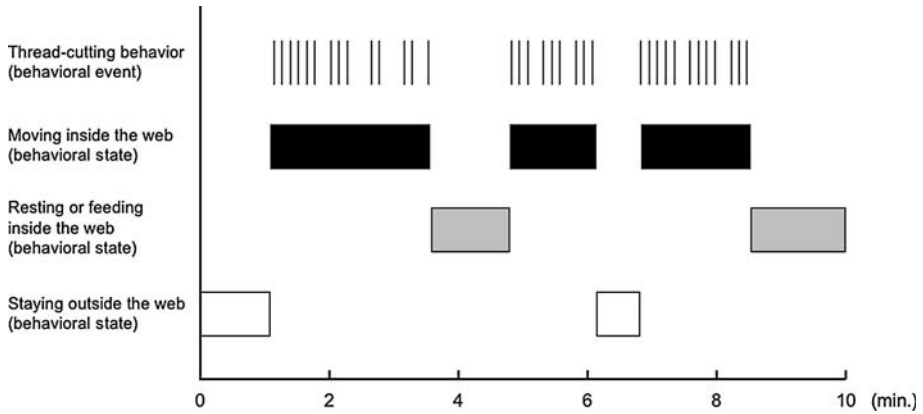


Fig. 1 Example of bar plots of a behavioral record in a 10-min. observation. Among the three behavioral states, they are exclusive. However, between a behavioral state (moving) and the instantaneous behavioral event (thread-cutting) exhibited inside the web, they occur simultaneously. For further details of bar plots dealing with overlapping behavioral data, see Haccou and Meelis (1992)

web, (2) resting or feeding inside the web: resting inside the web without any evident action except for grooming behavior or consuming a spider mite in the web, and (3) staying outside the web: moving, resting or feeding outside the web.

Predators often contact silken threads when they move inside a complex web. Just after contact, they cut silken threads quickly (in <1 s per thread), without halting their movements. This means that thread-cutting behavior does not only occur instantaneously, but also occurs simultaneously with the behavioral state of moving inside the web (Fig. 1). Because of the difficulty in recording the duration of thread-cutting behavior, we investigated the number of silken threads severed during the movement inside the web, to be able to roughly estimate the efficiency of thread-cutting behavior. We also investigated whether each silken thread was severed by chelicerae and palps, by the first pair of legs, and or by both. Twenty individuals were tested for each.

Statistics

A likelihood ratio test using a contingency table was adopted to compare the time of behavioral response in complex webs (Sokal and Rohlf 1995). To roughly estimate the efficiency of thread-cutting behavior, we used analysis of covariance (ANCOVA, Sokal and Rohlf 1995): the null hypothesis is that the total number of silken threads severed inside the web (the dependent variable) does not differ significantly among the predator species (the factor), when it is adjusted for the total duration of moving inside the web during the experimental period (the covariate). We used the Kruskal–Wallis test for a comparison of the number of prey consumed during the experimental period, since data lacked normality and homoscedasticity after transformation. Each analysis was performed with JMP (version 5.0.1 J, SAS Institute Inc., Cary, NC, USA).

Results and discussion

In this study, we did not find any major differences among the three predator species in behavioral response to the complex web of *T. urticae*. Each predator species exhibited a

strong tendency to enter and remain in the web (Fig. 2), and thus there was no significant difference among them in the proportion of total time staying inside the web (i.e., moving inside the web + resting or feeding inside the web) to that staying outside the web (likelihood ratio test, $df = 2$, $\chi^2 = 5.272$, $P = 0.0716$). All the predators of each species found and handled prey easily after entering the web (data not shown), although predation rates were low due to the short experimental period (10 min.) [$N = 20$ each, average (\pm SE); *N. californicus*: 0.60 ± 0.134 , *N. womersleyi*: 0.30 ± 0.105 , *P. persimilis*: 0.65 ± 0.182 , Kruskal-Wallis test, $df = 2$, $H = 2.891$, $P = 0.236$]. These results are in agreement with previous studies reporting that the behavioral pattern of staying inside a complex web confers several selective advantages on specialist predatory mites. As to the advantages of foraging, for example, they can exploit profitable food resources that are concentrated inside complex webs (Sabelis 1985; Ryoo 1986). They can also use the silken threads of complex webs for prey location on plants (Schmidt 1976). Furthermore, different advantages of exploiting complex webs are reported: *P. persimilis* usually oviposit, as well as reside, inside the webs of *T. urticae*, which gives protection to their offspring, as well as themselves, from predaceous arthropods (Roda et al. 2000, 2001). Dense complex webs of *T. pueraricola* protected all developmental stages of *N. womersleyi* and *N. californicus* to some degree from attacks by larger generalist insect predators, such as the big-eyed bugs *Piocoris varius* and the anthocorid predator *Orius sauteri*, on Kuzdu vine plants in a field (Shimoda et al. unpublished).

All individuals of the three predator species exhibited thread-cutting behavior during their movements inside complex webs (Fig. 3a, b). For example, when the predators contacted (sticky) silken threads inside the web, they usually first caught one or more silken threads with pairs of palps and then grasped them with pairs of their chelicerae, without halting their movements. Side-to-side movements of the chelicerae cut or ripped the thread(s). Although *N. womersleyi* sometimes cut one or more silken threads using only

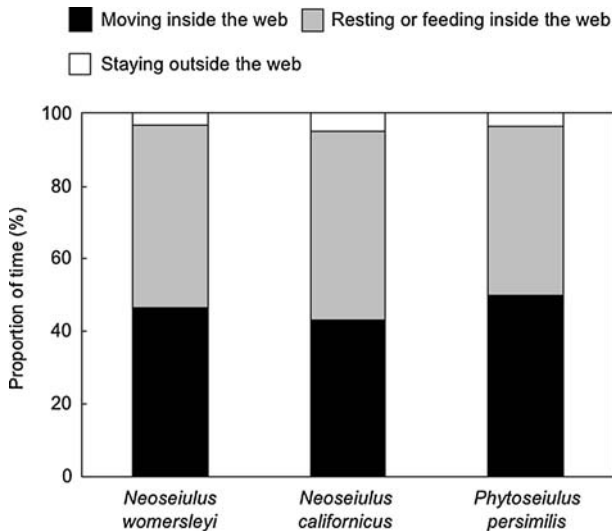


Fig. 2 Duration of each behavioral state by the three predatory mites (*Neoseiulus womersleyi*, *N. californicus*, and *Phytoseiulus persimilis*) exhibited inside or outside the complex web of *Tetranychus urticae*. Total duration of each observation was 10 min. Behavioral states inside or outside the web were divided into three categorizes

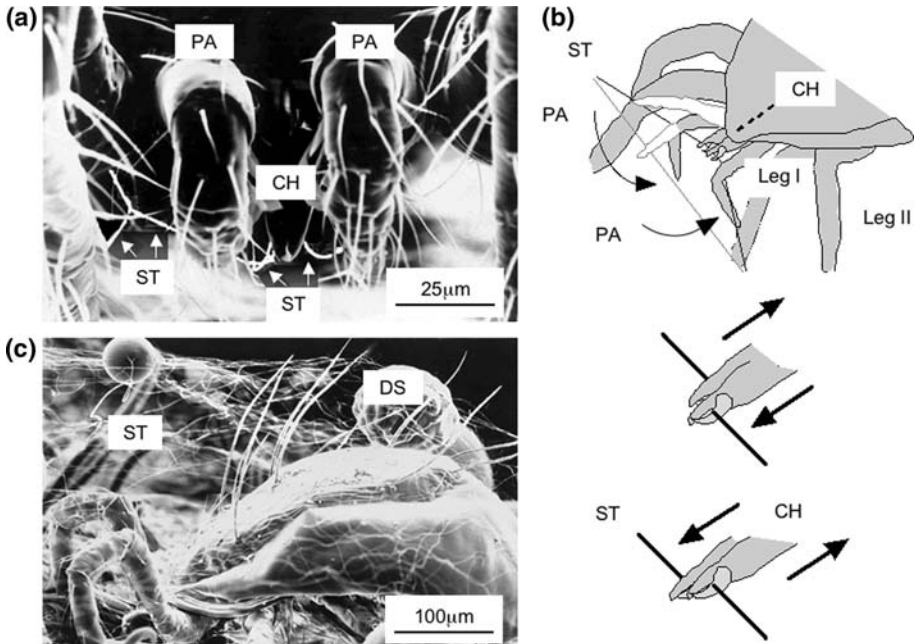


Fig. 3 **a, b** Thread-cutting behavior exhibited by *Phytoseiulus persimilis* while moving inside a complex web of *Tetranychus urticae*. The predator first catches a silken thread (ST) by holding it with a pair of palps (PA) and then grasps the thread with a pair of chelicerae (CH). The predator quickly cut it (<1 s.) by side-to-side movements of the chelicerae. **c** Long dorsal setae (DS), functioning as a pantograph, allow the predator to advance through the sticky silken threads (Sabelis and Bakker 1992). Photographs have been processed to make the silken threads more visible

the chelicerae, there was no major difference among the predator species in the basic pattern of thread-cutting behavior, i.e., cutting or ripping threads using their chelicerae and palps. Each predator species cut a thread quickly and easily, usually in <1 s. We observed adult females, males and immatures (at least nymphal stage) of the three predator species to exhibit the same behavior when entering and moving inside the complex webs of *T. urticae*, *T. kanzawai*, *T. pueraricola*, *T. phaseolus*, and *T. ludeni* on kidney bean leaves (Shimoda et al. unpublished). In Phytoseiid predatory mites, palps are sensory organs for the detection of prey (Chant 1985). The chelicerae, on the other hand, are grasping organs for capturing and eating prey (Chant 1985; Flechtmann and McMurtry 1992), though they are also a mating organ in adult males, used for transferring spermatophoral material to adult females (Amano and Chant 1978). Thus, this is the first report to propose an additional function of the palps and chelicerae, as organs for holding and cutting, respectively, in thread-cutting behavior.

Although the importance of specialist predatory mites in the biological control of *Tetranychus* mites has been well documented in past decades (McMurtry et al. 1970; Helle and Sabelis 1985; McMurtry and Croft 1997), how they open and smooth their way to accomplishing the task of efficiently exploiting prey inside complex webs is poorly understood. From the results in this study, we may consider the subject under the following three headings. First, our observations are in agreement with the review of Sabelis and Bakker (1992) who have identified the importance of dorsal setae in predatory mites. We observed

that the long dorsal setae of the three predator species sometimes assisted their movements, in spite of not being evaluated quantitatively, without getting entangled in sticky silken threads (Fig. 3c). Secondly, our observations also support the study of Montserrat et al. (2008) showing that thread-cutting behavior is effective in invading spider-mite webs. They have reported that *N. californicus* makes a hole (which they call a “triangular opening”) with this behavior when invading a web nest provided by *O. perseae*. In this study, each of the three predator species also broke several silken threads to be able to penetrate into the web. We observed in our preliminary investigations that *N. californicus*, *N. womersleyi* and *P. persimilis* created “spindle-shaped holes and slits” when penetrating or exiting a dense complex web produced by *T. urticae* (see Fig. 4 and the video). The shape of such openings is variable. Spindle-shaped holes, for example, sometimes change into “oval-shaped holes” after several predatory mites or spider mites have accessed the entrances. Thirdly, thread-cutting behavior by each predator species seems to be effective in reducing the adverse effects of the complex webs. Each predator species cut many silken threads while moving inside a complex web (Fig. 5a), and a strong relationship was detected between total duration of movement inside the web and the number of silken threads severed in each species (*N. californicus*: $y = 2.036 + 0.1199x$, $r^2 = 0.646$, $F = 35.725$, $df = 1, 18$, $P < 0.001$; *N. womersleyi*: $y = 7.999 + 0.0733x$, $r^2 = 0.552$, $F = 24.404$, $df = 1, 18$, $P < 0.001$; *P. persimilis*: $y = -9.937 + 0.1416x$, $r^2 = 0.412$, $F = 14.325$, $df = 1, 18$, $P < 0.01$; Fig. 5b). The results indicate that each predator species cut silken threads to be able to move inside a complex web. The ANCOVA result shows that the number of silken threads severed does not differ significantly among predator species when it is adjusted for the total duration of moving inside the web as the covariate (Table 1), suggesting that there is no major difference in the efficiency of thread-cutting behavior among them. Their frequent thread-cutting sometimes resulted in the construction of a network of “galleries” in a dense complex web, identified in our preliminary investigations (an entrance of galleries can be seen in

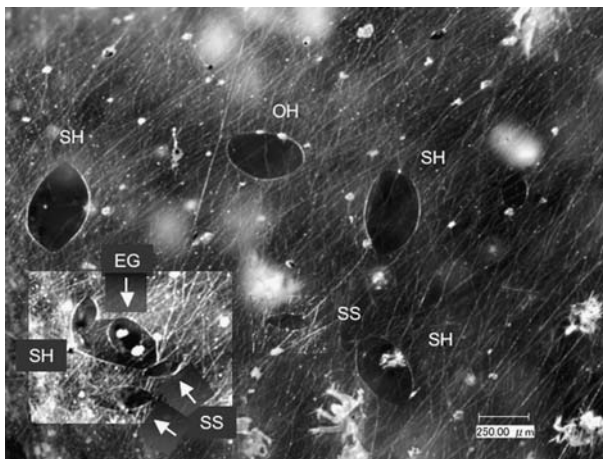


Fig. 4 Spindle-shaped holes (SH) and slits (SS) created by *Neoseiulus californicus* on the surface of a dense complex web of *Tetranychus urticae* on a leaf quadrate of kidney bean. The shape of such openings is variable, with one type being oval (OH). An entrance of galleries (EG) constructed inside the web. This photograph (also the video) was taken using a digital microscope system (KEYENCE, VHX-900). For more details, see the text and video

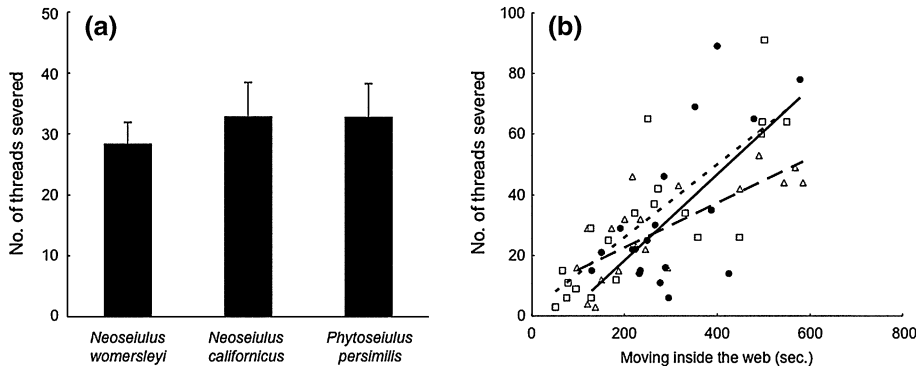


Fig. 5 **a** Total numbers (mean \pm SE) of silken threads severed by each of three predatory mites while moving inside a complex web of *Tetranychus urticae* during the 10-m. experimental period. **b** Total number of silken threads severed for each predatory mite (*Neoseiulus womersleyi*: open triangles, dashed line; *N. californicus*: open squares, dotted line; *Phytoseiulus persimilis*: filled circles, solid line) as a function of total duration of moving inside the web. The separate regressions do not differ in slope, and the pooled regression is highly significant (see “factor \times covariate” and “covariate” in Table 1, respectively), which permits carrying out an ANCOVA (Sokal and Rohlf 1995)

Table 1 ANCOVA results for effect of predator species on total number of silken threads severed, when taking the covariate (total duration of moving inside the web) into account

Source	df	Mean square	F-value	P-value
Predator	2	239.642	1.047	0.3577
Moving inside the web	1	14,186.562	61.999	< 0.0001
Error	56	228.819		

The interaction between predator species (factor) and total duration of moving inside the web (covariate) did not contribute significantly to the model (df = 2, 54, $F = 2.099$, $P = 0.1324$) and was therefore removed

both Fig. 4 and the video), which are likely to play an important role in their successful movements inside the web.

As mentioned earlier, *N. californicus* is reported to use their first legs when ripping and destroying the wall of a web-nest constructed by *O. perseae* (Montserrat et al. 2008). In contrast, this type of thread-cutting behavior was never observed in the three predator species when invading complex webs of *T. urticae*. One possible explanation may be that *N. californicus* adopts different types of thread-cutting behavior in response to the type of spider mite web it is attacking (i.e., complex webs vs. nest webs). Alternatively, their thread-cutting behavior might be dependent on the density of silken threads within spider mite webs. For example, the adult coccinellid predator *Stethorus japonicus* normally uses its mandibles when faced with the coarse, loosely jointed complex webs of *T. urticae*, whereas it uses its first legs in addition to its mandibles when facing denser, more complex web structures (Shimoda et al. unpublished). Further systematic studies are needed to clarify how each predator species copes behaviorally with different types of spider mite webs, which will shed new light on past interpretations of their interactions in the field.

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References

- Amano H, Chant DA (1978) Mating behaviour and reproductive mechanisms of two species of predacious mites, *Phytoseiulus persimilis* Athias-Henriot and *Amblyseius andersoni* (Chant) (Acarina: Phytoseiidae). *Acarologia* 20:196–213
- Chant DA (1985) External anatomy. In: Helle W, Sabelis MW (eds) Spider mites: their biology, natural enemies and control. World crop pests, vol 1B. Elsevier, Amsterdam, pp 5–9
- Flechtmann CHW, McMurtry JA (1992) Studies on how phytoseiid mites feed on spider mites and pollen. *Int J Acarol* 18:157–162
- Gerson U (1979) Silk production in *Tetranychus* (Acari: Tetranychidae). In: Rodriguez JG (ed) Recent advances in acarology, vol 1. Academic Press, New York, pp 177–188
- Gerson U (1985) Webbing. In: Helle W, Sabelis MW (eds) Spider mites: their biology, natural enemies and control. World crop pests, vol 1A. Elsevier, Amsterdam, pp 223–232
- Gilstrap FE, Oatman ER (1976) The bionomics of *Scolothrips sexmaculatus* (Pergande) (Thysanoptera: Thripidae), an insect predator of spider mites. *Hilgardia* 44:27–59
- Haccou P, Meelis E (1992) Statistical analysis of behavioural data: an approach based on time-structured models. Oxford University Press, Oxford
- Helle W, Sabelis MW (1985) Spider mites: their biology, natural enemies and control. World crop pests, vol 1B. Elsevier, Amsterdam
- McMurtry JA, Croft BA (1997) Life-styles of phytoseiid mites and their roles in biological control. *Annu Rev Entomol* 42:291–321. doi:10.1146/annurev.ento.42.1.291
- McMurtry JA, Johnson HG (1966) An ecological study of the spider mite *Oligonychus punicae* (Hirst) and its natural enemies. *Hilgardia* 37:363–402
- McMurtry JA, Scriven GT (1964) Studies on the feeding, reproduction, and development of *Amblyseius hibisci* (Acarina: Phytoseiidae). *Ann Entomol Soc Am* 58:48–56
- McMurtry JA, Huffaker CB, Van de Vrie M (1970) Ecology of tetranychid mites and their natural enemies: a review I. Tetranychid enemies: their biological characters and the impact of spray practices. *Hilgardia* 40:331–390
- Montserrat M, Peña FDL, Hormaza JJ, González-Fernández JJ (2008) How do *Neoseiulus californicus* (Acari: Phytoseiidae) females penetrate densely webbed spider mite nests? *Exp Appl Acarol* 44:101–106. doi:10.1007/s10493-008-9137-y
- Oku K, Yano S, Takafuji A (2003) Spider mite's use of a refuge during the quiescent stage in the presence of a predator. *Entomol Exp Appl* 108:71–74. doi:10.1046/j.1570-7458.2003.00069.x
- Oku K, Yano S, Takafuji A (2004) Nonlethal indirect effects of a native predatory mite, *Amblyseius womersleyi* Schicha (Acarina: Phytoseiidae), on the phytophagous mite *Tetranychus kanzawai* Kishida (Acari: Tetranychidae). *J Ethol* 22:109–112. doi:10.1007/s10164-003-0102-2
- Osakabe M (1988) Relationships between food substances and development success in *Amblyseius sojaensis* Ehara (Acarina: Phytoseiidae). *Appl Entomol Zool (Jpn)* 23:45–51
- Putnam WL (1955) Bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. *Can Entomol* 87:9–33
- Putnam WL (1962) Life-history and behaviour of the predacious mite *Typhlodromus (T.) caudiglans* Schuster (Acarina: Phytoseiidae) in Ontario, with notes on the prey of related species. *Can Entomol* 94:163–177
- Roda A, Nyrop J, Dicke M, English-Loeb G (2000) Trichomes and spider-mite webbing protect predatory mite eggs from intraguild predation. *Oecologia* 125:429–436. doi:10.1007/s004420000462
- Roda A, Nyrop J, English-Loeb G, Dicke M (2001) Leaf pubescence and two-spotted spider mite webbing influence phytoseiid behavior and population density. *Oecologia* 129:551–560
- Ryoo MI (1986) Studies on the basic components of the predation of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). *Res Popul Ecol (Kyoto)* 28:17–26. doi:10.1007/BF02515531
- Sabelis MW (1985) Predation on spider mites. In: Helle W, Sabelis MW (eds) Spider mites: their biology, natural enemies and control. World crop pests, vol 1A. Elsevier, Amsterdam, pp 103–1129
- Sabelis MW, Bakker FM (1992) How predatory mites cope with the webs of their tetranychid prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp Appl Acarol* 16:203–225. doi:10.1007/BF01193804

- Saito Y (1985) Life types of spider mites. In: Helle W, Sabelis MW (eds) Spider mites: their biology, natural enemies and control. World crop pests, vol 1A. Elsevier, Amsterdam, pp 253–264
- Schmidt G (1976) Der Einfluss der von den Beutetieren hinterlassenen Spuren auf Suchverhalten und Sucherfolg von *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). Z Angew Entomol 82:216–218
- Shimoda T, Shinkaji N, Amano H (1997) Prey stage preference and feeding behavior of *Oligota kashmirica benefica* (Coleoptera: Staphylinidae), an insect predator of the spider mite *Tetranychus urticae* (Acari: Tetranychidae). Exp Appl Acarol 21:665–675
- Shimoda T, Kishimoto H, Amano H, Takabayashi J (2003) Behavioral adaptation of predatory mites to move within complex webs of spider mites. Abstracts of the annual meeting of the Japanese Society of Applied Entomology and Zoology, vol 47, p 110 (in Japanese). Available via J-STAGE. http://www.jstage.jst.go.jp/browse/ajsaez/47/0/_contents
- Sokal RR, Rohlf FJ (1995) Biometry, 3rd edn. W. H. Freeman, New York
- Takafuji A, Chant DA (1976) Comparative studies of two species of predacious phytoseiid mites (Acarina: Phytoseiidae), with special reference to their responses to the density of their prey. Res Popul Ecol (Kyoto) 17:255–310. doi:10.1007/BF02530777
- Trichilo PJ, Leigh TF (1986) Predation on spider mite eggs by the western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. Environ Entomol 15:821–825