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The stealthiness of predatory mites as spider mite biological control agents

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Abstract

Adult spider mite females that are aware of predatory mites can reduce predation by dispersing from patches invaded by predators or by shifting their oviposition site onto webs where eggs are predated less than on leaf surfaces. Therefore, the stealthiness of predatory mites stalking spider mite females should largely determine the success of spider mite control. This study examined the stealthiness of three predatory mites: *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* McGregor, and *Neoseiulus womersleyi* Schicha. The first two species have been commercialized as spider mite biological control agents, whereas the last species is a native predator of spider mites in Japan. We measured two indices of predator stealthiness in bioassays using *Tetranychus kanzawai* Kishida as prey: the proportion of prey mites that dispersed from their patches in response to predator intrusion and the proportions of prey eggs laid on webs in response to predator eggs. Both indices resulted in the same ranking, with *P. persimilis* ranking highest and *N. womersleyi* lowest. The greater stealthiness of *P. persimilis* eggs compared with *N. womersleyi* eggs seemed to be due to the lower amount of detectable substances on the egg surface. We also measured this index of stealthiness for European and Japanese *Tetranychus urticae* Koch populations and found that they had the same

25 stealthiness ranking as measured using *T. kanzawai*. Therefore, we predict that the stealthiness of
26 predatory mites is consistent across prey species and could be an effective index, along with
27 conventional indices, for evaluating predatory mites as spider mite biological control agents.

28

29 **Keywords** biological control agent ■ *Phytoseiulus persimilis* ■ *Neoseiulus californicus* ■ *Neoseiulus*
30 *womersleyi* ■ *Tetranychus kanzawai* ■ *Tetranychus urticae*

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1. Introduction

Predation becomes difficult when the threatened prey adopts defensive behaviors or traits before the attack (Tollrian and Harvell, 1999). Therefore, predators have developed various ways to reduce the probability of being detected by their prey, such as creeping and aggressive mimicry (Wickler, 1968). From this perspective, stealthiness could be one such key to predation success.

The spider mites *Tetranychus urticae* and *T. kanzawai* are tiny arthropod pest species that cause severe economic damage to hundreds of agricultural crops across many plant families (Jeppson et al., 1975, Zhang, 2003). In particular, the ability of *T. urticae* to develop resistance to newly introduced pesticides has caused ongoing problems for agricultural production (Croft and van de Baan, 1988). Although these two mites have many host plant species in common, they differ in several ecological traits such as dispersal timing from infested patches (Oku et al., 2002) and conditions for entering reproductive diapause (Oku et al., 2003). Spider mites in the genus *Tetranychus* construct three-dimensional protective webs on leaf surfaces and usually feed and oviposit on the leaf surface under these webs (Saito, 1983). Some predatory mite species can invade the webs and consume spider mites (McMurtry et al., 1970, Sabelis and Bakker, 1992, McMurtry and Croft, 1997, McMurtry et al., 2013). When adult female spider mites are aware of predatory mites, the females leave the patches containing predators (Bernstein, 1984, Grostal and Dicke, 1999, Oku et al., 2004, Škaloudová et al., 2007, Bowler et al., 2013) and disperse farther and scatter more than mites dispersing in response to resource deterioration (Otsuki and Yano, 2014a, 2014b). Moreover, adult female spider mites that are aware of predatory mites can reduce predation by shifting their oviposition site onto the webs (Oku and Yano, 2007, Lemos et al., 2010) where eggs are predated less than those on leaf surfaces (Otsuki and Yano, 2017). Therefore, whether predatory mites are detected by spider mites should largely determine the success of biological control of spider mites using predatory mites.

The utility of predatory mites as spider mite biological control agents has conventionally been evaluated using indices such as the predation rate and intrinsic rate of natural increase (*e.g.*, Janssen and Sabelis, 1992, Gotoh et al., 2006). These indices are measured under laboratory conditions where neither spider mites nor predatory mites have opportunities for dispersal. Under such conditions, the predatory mites eventually consume all of the spider mites, even if the prey is aware of the predators and tries to disperse from the patch. Therefore, the conventional indices may fail to reflect possible differences in predator stealthiness to spider mites. Moreover, rearing experimental animals under laboratory conditions usually deprives them of dispersal opportunities, so we must always remember that we may observe artifacts under experimental conditions, *i.e.*, behaviors of target experimental animals that would otherwise have dispersed from the patch.

To quantify predator stealthiness to spider mites, we measured the proportion of mated female spider mites (*i.e.*, the dispersing stage) that dispersed from their webs in response to predator intrusion using a setup allowing prey dispersal. We also measured the proportions of spider mite eggs laid on webs in response to predatory mite eggs. We used *T. kanzawai* as the prey species, as this species has been reported to disperse (Oku et al., 2004, Bowler et al., 2013) or shift oviposition sites onto webs (Oku and Yano, 2007, Otsuki and Yano, 2017) in response to predatory mites. As predatory mites, we examined two commercialized biological control agents used against spider mites of the genus *Tetranychus*: *Phytoseiulus persimilis* (Hussey and Bravenboer, 1971) and *Neosiulus californicus* (Cooping, 2001). We also examined *N. womersleyi*, which is a native predator of *T. kanzawai* in Japan (Hamamura, 1986), but has not been commercialized as a biological control agent. *Neoseiulus womersleyi* can invade *T. kanzawai* webs (Oku et al., 2004), and can control *T. kanzawai* populations under certain conditions (Kondo, 2004). To examine whether stealthiness is affected by the species and populations of spider mite used, we also measured the anti-predator behaviors of European and Japanese populations of a related spider mite,

T. urticae. Based on these results, we discuss whether the degree of stealthiness is consistent across species and populations of prey mites.

2. Materials and Methods

2.1 Mites

The *T. kanzawai* study population was collected in September 2014 in Kyoto, Japan, and was reared on expanded primary leaves of kidney bean (*Phaseolus vulgaris* L.), which were cut from the petiole and pressed onto water-saturated cotton in Petri dishes (“leaf discs”). The water-saturated cotton served as a barrier to prevent the mites from escaping, and all experimental setups were placed on water-saturated cotton. The leaf discs were placed in transparent plastic containers maintained at $25 \pm 1^\circ\text{C}$, $50 \pm 1\%$ relative humidity, and a 16L (7:00–23:00):8D photoperiod. All experiments were conducted under these laboratory conditions. The study populations of *T. urticae* were collected in 2008–2009 in the northern Netherlands (European population, Khajehali et al., 2011) and in 1998 in Nara, Japan (Japanese population). These populations were maintained in the manner described above.

We obtained a population of *P. persimilis* from a commercial source in Europe (Koppert Biological Systems, The Netherlands), and maintained the population for more than 10 years on kidney bean (*Phaseolus vulgaris*) leaf discs that were heavily infested with *T. urticae* (Japanese population) as prey. Therefore, the population should not have a coevolutionary history with *T. kanzawai*, which occurs only in Asia (Ehara, 1999). The *N. californicus* study population was collected in 2000 in Nagano, Japan, and that of *N. womersleyi* in 2014 in Kyoto, Japan. These populations were reared on bean leaf discs in the same manner.

2.2 Dispersal of *T. kanzawai* females in response to predator intrusion

105 To quantify the stealthiness of predatory mites, we first examined the predator-induced dispersal of
106 *T. kanzawai* females. To investigate the within- and between-patch dispersal of *T. kanzawai* females
107 in response to predator intrusion, we introduced three mated *T. kanzawai* females 2 days after
108 maturation onto 10×10 -mm² bean leaf squares artificially bent 90° (Fig. 1). After 24 h, when the
109 leaf harbored ample prey eggs and three-dimensional webs, two of the three females were removed.
110 Then, we introduced a mated female of one of the three predatory mite species onto each bent leaf.
111 The predators had previously been starved by isolation for 48 h in 1.5-mL microtubes (Biorambo
112 Microtube, As One, Osaka, Japan) with a water droplet. The tubes had sufficient ventilation for mite
113 survival. The bent leaf and ample eggs and webs thereon were intended to prevent dispersal of the
114 predators that are not accustomed to the new conditions. Ample prey eggs were also intended to
115 delay predation on *T. kanzawai* females because predators seldom attack prey females as long as
116 prey eggs are available. For comparison, we also prepared bent leaves without adding a predator
117 (*i.e.*, keeping a *T. kanzawai* female only), which served as a control. During the next 30 min, no *T.*
118 *kanzawai* female was preyed upon by the predator that settled under the spider mite webs. We then
119 placed a 10×10 -mm² uninfested bean leaf square close to the original bent leaf square so as to form
120 an initial patch with a bent square. The uninfested leaf square was connected to another $10 \times$
121 10 -mm² uninfested leaf square (trap) by a non-food substrate (30×10 -mm² Parafilm, Parafilm M;
122 American National Can, Chicago, IL, USA) (Fig. 1). Because *T. kanzawai* females are not attracted
123 to a 10×10 -mm bean square at a distance of 30 mm (Otsuki and Yano, 2014b), females found on
124 the trap square were considered to have abandoned the initial patch, and not to have been attracted
125 by the trap. The experimental setup was kept under laboratory conditions, and the position and
126 survival status of both the *T. kanzawai* female and predatory mite were recorded at 10:00, 13:00,
127 16:00, 19:00, and 22:00 for 3 days, after which predator offspring began to hatch. We stopped the
128 observations when the *T. kanzawai* female had dispersed either within or between patches before 3

days had elapsed. We considered a *T. kanzawai* female to have dispersed within the patch if an uninfested area of the initial patch contained webs, injury scars, feces, and eggs, regardless of the presence of the female, whereas we considered the female to have dispersed between patches if the trap contained these signs. There were 39 replicates without a predator, 43 with *P. persimilis*, 45 with *N. californicus*, and 45 with *N. womersleyi*.

The proportion of *T. kanzawai* females that had dispersed from the bent leaf squares (both within- and between-patch) in response to each predatory mite species was compared with the control without a predator using Fisher's exact test. The proportion of *T. kanzawai* females preyed upon during the experiment was compared among predatory mite species using Fisher's exact test. The Holm–Bonferroni correction was used to adjust *P*-values for multiple comparisons. The statistical analyses were performed using R v.3.2.2 (R Foundation for Statistical Computing, Vienna, Austria).

2.3 Oviposition site selection of spider mites in response to predator eggs

As another stealthiness index of predatory mites, we examined the proportions of spider mite eggs laid on webs in response to predator eggs. We did not use adult predators in this experiment because they consume spider mite eggs, making it impossible to calculate the proportion of eggs on the webs.

Based on the method of Oku and Yano (2007), $10 \times 10\text{-mm}^2$ bean leaf squares were bent to standardize the patch structure used for building spider mite webs (Fig. 2). Then, we obtained eggs of the three predatory mite species within 24 h of oviposition and transferred three eggs of one species onto the bottom of the bent leaf surfaces. Next, we introduced a mated *T. kanzawai* female 2 days after maturation onto the bent leaf. After 24 h, we counted the number of eggs laid on both the leaf surface and the web. The proportions of *T. kanzawai* eggs laid on webs were compared among

the predatory mite species using the Steel–Dwass test. There were 42 replicates with *P. persimilis* eggs, 38 with *N. californicus* eggs, and 41 with *N. womersleyi* eggs.

To examine whether concealing or detectable surface materials were responsible for the different degrees of stealthiness, eggs of *P. persimilis* (least detectable, see Results) and *N. womersleyi* (most detectable, see Results) were dipped in kitchen detergent (Kyukyutto; Kao, Tokyo) diluted 10-fold with water. After 10 s, the eggs were rinsed with a fine brush in ample distilled water for 10 s to remove the detergent from the eggs. Since the detergent is for dishwashing, it should be completely removed by rinsing in water. We first confirmed that the treatment did not have harmful effects on predatory mite eggs. The proportions of *T. kanzawai* eggs laid on webs in response to three untreated or washed eggs of the respective predator species were measured in the manner described above. We hypothesized that removing the surface materials would make the washed *P. persimilis* eggs more detectable (resulting in more oviposition on webs) if the materials served as concealment, whereas detectable surface materials should make the washed *N. womersleyi* eggs less detectable (resulting in less oviposition on webs). The proportions were compared between untreated and washed eggs using the Mann–Whitney *U*-test. There were 39 replicates with untreated *P. persimilis* eggs, 37 with washed *P. persimilis* eggs, 38 with untreated *N. womersleyi* eggs, and 43 with washed *N. womersleyi* eggs.

To examine whether the stealthiness index is consistent across prey mites or is affected by the species and origins of the prey populations used, we also examined the oviposition site pattern using a related spider mite, *T. urticae*. Because the *P. persimilis* used originated from Europe, while *N. californicus* and *N. womersleyi* are from Japan, we used European and Japanese populations of *T. urticae* to examine this question. The proportions of eggs laid on webs were examined in the manner described above and compared among predatory mite species for the various *T. urticae* populations using the Steel–Dwass test. There were 36 replicates with *P. persimilis* eggs, 33 with *N. californicus*

eggs, and 34 with *N. womersleyi* eggs for the European *T. urticae* population, as well as 31, 34, and 35, respectively, for the Japanese *T. urticae* population.

3. Results

3.1 Dispersal of *T. kanzawai* females in response to predator intrusion

The within-patch dispersal of *T. kanzawai* females in response to *P. persimilis* and *N. womersleyi* did not significantly differ from that of the control without predators. Only within-patch dispersal in response to *N. californicus* was significantly lower than that of the control (Fig. 3a). Between-patch dispersal of *T. kanzawai* females in response to *P. persimilis* and *N. californicus* did not significantly differ from that of the control, whereas between-patch dispersal in response to *N. womersleyi* was significantly higher than that of the control (Fig. 3b). In addition, the proportion of *T. kanzawai* females preyed upon by *P. persimilis* was the highest, while that by *N. womersleyi* was the lowest. The differences were significant between all pairs of predatory mite species (Fig. 4).

3.2 Oviposition site selection of spider mites in response to predator eggs

The proportions of *T. kanzawai* eggs laid on webs in response to *N. womersleyi* were the highest (the least stealthy), while that in response to *P. persimilis* was the lowest (the greatest stealthiness). Significant differences were found between all pairs of predatory mite species (Fig. 5).

The proportions of *T. kanzawai* eggs laid on webs in response to washed *P. persimilis* eggs were slightly lower than that in response to untreated eggs (Fig. 6a), whereas those in response to washed *N. womersleyi* eggs were considerably lower than that in response to untreated *N. womersleyi* eggs (Fig. 6b). These results suggest the existence of detectable, rather than concealing, surface materials on *N. womersleyi* eggs.

The proportions of eggs deposited on webs by *T. urticae* females of European and Japanese populations in response to predatory mite eggs showed the same pattern seen using *T. kanzawai* females. Significant differences were found between all pairs, except for the *N. californicus* and *N. womersleyi* pair examined with the European *T. urticae* population and the *P. persimilis* and *N. californicus* pair examined with the Japanese *T. urticae* population (Fig. 7).

4. Discussion

We systematically measured stealthiness indices of predatory mites, the proportion of prey mites dispersed from their patches in response to predator intrusion, and the proportions of prey eggs laid on webs in response to predator eggs in environments where predator-induced dispersal and oviposition site shifts onto webs are possible. We found that both indices resulted in the same ranking across prey species and prey populations, with *P. persimilis* ranking highest and *N. womersleyi* lowest.

Tetranychus kanzawai females dispersed from patches intruded upon by *N. womersleyi*, but did not disperse from patches intruded upon by *P. persimilis* or *N. californicus*. If this result was due to the relatively low predation rate by *N. womersleyi*, compared to the other two predator species (Fig.4), then we should have obtained the highest proportion of dispersed *T. kanzawai* females in the absence of predation (*i.e.* control). In contrast, the proportion of *T. kanzawai* females that dispersed from control patches did not differ from those in response to *P. persimilis* or *N. californicus*. Therefore, we may reasonably conclude that *T. kanzawai* females were less aware of *P. persimilis* and *N. californicus* than of *N. womersleyi*, and hence more females were preyed upon by the former two predator species. *Neoseiulus womersleyi* promoted the between-patch dispersal of prey mites, which might in turn increase the number of prey patches.

Another stealthiness index of predatory mites, the proportions of spider mite eggs laid on webs in response to predator eggs, showed the same ranking, *i.e.*, the highest stealthiness in *P. persimilis* and lowest in *N. womersleyi*. Because all of the predatory mites oviposited during the experiments examining spider mite dispersal, the stealthiness index described above should in part reflect the stealthiness of the deposited predatory mite eggs. Moreover, the ranking of the stealthiness index was also consistent with both European and Japanese populations of *T. urticae*, indicating that the stealthiness of predatory mites is not affected by the origin of the spider mite or by the predatory mite populations tested. These results suggest that the relative levels of stealthiness are consistent across prey mite species, although their absolute values may depend on the specific combination of prey and predatory mite populations. Therefore, predator stealthiness could be used as a novel index to evaluate the utility of predatory mite populations as biological control agents.

The stealthiness indices of the two commercialized biological control agents, *P. persimilis* and *N. californicus*, were higher than those of *N. womersleyi*. This might not be coincidental if the two predatory mites had been adopted as biological control agents based on their empirical utility in crop fields, which should in part reflect their stealthiness to spider mites. In comparison, *N. womersleyi* seems relatively unsuitable as a biological control agent against spider mites because the predator failed to predate spider mites before dispersal, probably due to its low level of stealthiness (but see Kondo, 2004 for a successful case in a greenhouse).

Considering the higher stealthiness of the other two species, *N. womersleyi* might have potential for improved stealthiness. The low stealthiness (high detectability) of *N. womersleyi* eggs seemed to be due to the existence of detectable surface materials rather than to the lack of special concealing materials (Fig. 6b). Although *N. womersleyi* has much lower stealthiness than *P. persimilis* and *N. womersleyi*, the mite thrives under natural conditions involving predation of spider mites (McMurtry and Croft, 1997). Therefore, the inability of *N. womersleyi* to reduce such

apparently maladaptive materials suggests that the materials have unknown adaptive functions,
which remain to be addressed in future investigations.

The fitness of animals is largely affected by between-patch dispersal in environments where
opportunities to disperse are ensured (Bonte et al., 2012). Adult female spider mites disperse
between food patches primarily by walking (Brandenburg and Kennedy, 1982, Kennedy and Smitley,
1985, Margolies and Kennedy, 1985), although they disperse farther in response to predators
(Otsuki and Yano, 2014b). Dispersed spider mite females can establish local populations, which are
often in danger of extinction because of larger predatory insects (Janssen et al., 1998), coincidental
intra-guild predation by larger herbivores (Shiotsuka and Yano, 2012), and natural or
human-induced disturbance (*e.g.*, Das, 1959). Therefore, between-patch spider mite dispersal in
response to predatory mites with low stealthiness should in turn reduce the extinction rate of spider
mite metapopulations in the long term by increasing the number of local populations (Levins, 1969).
Although predator-induced prey dispersal seems maladaptive for predator individuals in the short
term, it may contribute to a stable prey supply for future offspring habitats. In other words,
predatory mites with low stealthiness may ‘pasture’ female prey mites, as long as prey eggs are
abundant within the intruded patch. Therefore, it is necessary to discuss whether high/low
stealthiness is advantageous to predatory mites in light of the metapopulation dynamics of both prey
and predatory mites.

Author Contribution Statement

HO and SY conceived and designed experiments. HO conducted experiments, and analyzed data.
HO and SY wrote the manuscript.

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274

275 **Conflict of interest**

276 The authors declare no conflict of interest.
277

278 **References**

- 279 Bernstein, C., 1984. Prey and predator emigration responses in the acarine system *Tetranychus*
280 *urticae*-*Phytoseiulus persimilis*. *Oecologia* 61, 134–142. <https://doi.org/10.1007/BF00379099>
- 281 Bonte, D., Van Dyck H., Bullock J. M., Coulon A., Delgado M., Gibbs M., Lehouck V., Matthysen
282 E., Mustin K., Saastamoinen M., Schtickzelle N., Stevens V. M., Vandewoestijne S., Baguette M.,
283 Barton K., Benton T., Chaput-Bardy A., Clobert J., Dytham C., Hovestadt T., Meiner C. M.,
284 Palmer S. C. F., Turlure C., Travis J. M. J. 2012. Costs of dispersal. *Biol. Rev.* 87, 290–312.
285 <https://doi.org/10.1111/j.1469-185X.2011.00201.x>
- 286 Bowler, D. E., Yano S., Amano, H., 2013. The non-consumptive effects of a predator on spider mites
287 depend on predator density. *J. Zool.* 289, 52–59.
288 <https://doi.org/10.1111/j.1469-7998.2012.00961.x>
- 289 Brandenburg, R. L., Kennedy, G. G., 1982. Intercrop relationships and spider mite dispersal in a
290 corn/peanut agroecosystem. *Entomol. Exp. Appl.* 32, 269–276.
291 <https://doi.org/10.1111/j.1570-7458.1982.tb03217.x>
- 292 Cooping, L. G., (Ed) 2001. *The BioPesticide Manual*, 2nd ed. British Crop Protection Council,
293 Survey, p528.

- 294 Croft, B. A ., van de Baan, H. E., 1988. Ecological and genetic factors influencing evolution of
- 295 pesticide resistance in tetranychid and phytoseiid mites. *Exp. Appl. Acarol.* 4, 277 – 300.
- 296 <https://doi.org/10.1007/BF01196191>
- 297 Das, G. M., 1959. Bionomics of the tea red spider, *Oligonychus coffeae* Nietner. *Bull. Entomol. Res.*
- 298 50, 265–274. <https://doi.org/10.1017/S0007485300054572>
- 299 Ehara, S., 1999. Revision of the spider mite family Tetranychidae of Japan (Acari, Prostigmata).
- 300 *Species Diversity* 4:63-141.
- 301 Gotoh, T., Tsuchiya, A., Kitashima, Y., 2006. Influence of prey on developmental performance,
- 302 reproduction and prey consumption of *Neoseiulus californicus* (Acari: Phytoseiidae). *Exp. Appl.*
- 303 *Acarol.* 40, 189-204. <https://doi.org/10.1007/s10493-006-9032-3>
- 304 Grostal, P., Dicke, M., 1999. Direct and indirect cues of predation risk influence behavior and
- 305 reproduction of prey: a case for acarine interactions. *Behav. Ecol.* 10, 422–427.
- 306 <https://doi.org/10.1093/beheco/10.4.422>
- 307 Hamamura, T., 1986. Studies on the biological control of Kanzawa spider mite, *Tetranychus kanzawai*
- 308 Kishida by the chemical resistant predacious mite, *Amblyseius longispinosus* (Evans) in tea fields
- 309 (Acarina: Tetranychidae, Phytoseiidae). *Bull. Natl. Res. Inst. Tea* 21, 121–201.
- 310 Hussey, N. W., Bravenboer, L., 1971. Control of pests in glasshouse culture by the introduction of
- 311 natural enemies, in: Huffaker, C. B. (ed) *Biological Control*, Springer, Boston, pp. 195-216.
- 312 Janssen, A., Pallini, A., Venzon, M., Sabelis, M. W., 1998. Behaviour and indirect interactions in
- 313 food webs of plant-inhabiting arthropods. *Exp. Appl. Acarol.* 22, 497–521.
- 314 <https://doi.org/10.1023/A:1006089924336>
- 315 Janssen, A., Sabelis, M. W., 1992. Phytoseiid life-histories, local predator-prey dynamics, and
- 316 strategies for control of tetranychid mites. *Exp. Appl. Acarol.* 14, 233-250.
- 317 <https://doi.org/10.1007/BF01200566>

- 318 Jeppson, L. R., Keifer, H., H., Baker, E. W., 1975. Mites Injurious to Economic Plants. University of
319 California Press, Berkeley, CA, USA.
- 320 Kennedy, G. G., Smitley, D. R., 1985. Dispersal, in: Helle, W., Sabelis, M. W., (Eds.) Spider mites:
321 their biology, natural enemies and control, Elsevier, Amsterdam, pp. 233–251.
- 322 Khajehali, J., Van Nieuwenhuysse, P., Demaeght, P., Tirry, L., Van Leeuwen, T., 2011. Acaricide
323 resistance and resistance mechanisms in *Tetranychus urticae* populations from rose greenhouses
324 in the Netherlands. Pest. Manag. Sci. 2011. 67, 1424–1433. <https://doi.org/10.1002/ps.2191>
- 325 Kondo, A., 2004. Colonizing characteristics of two phytoseiid mites, *Phytoseiulus persimilis*
326 Athias-Henriot and *Neoseiulus womersleyi* (Schicha) (Acari: Phytoseiidae) on greenhouse
327 grapevine and effects of their release on the kanzawa spider mite, *Tetranychus kanzawai* Kishida
328 (Acari: Tetranychidae). Appl. Entomol. Zool. 39, 643–649. <https://doi.org/10.1303/aez.2004.643>
- 329 Lemos, F., Sarmiento, R. A., Pallini, A., Dias, C. R., Sabelis, M. W., Janssen, A., 2010. Spider mite
330 web mediates anti-predator behaviour. Exp. Appl. Acarol. 52, 1–10.
331 <https://doi.org/10.1007/s10493-010-9344-1>
- 332 Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for
333 biological control. Bull. Entomol. Soc. Am. 15, 237–240. <https://doi.org/10.1093/besa/15.3.237>
- 334 Margolies, D. C., Kennedy, G. G., 1985. Movement of the two spotted spider mite, *Tetranychus*
335 *urticae*, among hosts in a corn-peanut agroecosystem. Entomol. Exp. Appl. 37, 55–61.
336 <https://doi.org/10.1111/j.1570-7458.1985.tb03452.x>
- 337 McMurtry, J. A., Huffaker, C. B., Van de Vrie, M., 1970. Ecology of tetranychid mites and their
338 natural enemies: a review I. Tetranychid enemies: their biological characters and the impact of
339 spray practices. Hilgardia 40, 331–390. <https://doi.org/10.3733/hilg.v40n11p331>
- 340 McMurtry, J. A., Croft, B. A., 1997. Life-styles of phytoseiid mites and their roles in biological
341 control. Annu. Rev. Entomol. 42, 291–321. <https://doi.org/10.1146/annurev.ento.42.1.291>

- 342 McMurtry, J. A., De Moraes, G. J., Sourassou, N. F., 2013. Revision of the lifestyles of phytoseiid
343 mites (Acari: Phytoseiidae) and implications for biological control strategies. Syst. Appl. Acarol.
344 18, 297-320. <https://doi.org/10.11158/saa.18.4.1>
- 345 Oku, K., Yano, S., Takafuji, A., 2002. Different maternal effects on offspring performance in
346 Tetranychid mites, *Tetranychus kanzawai* and *T. urticae* (Acari: Tetranychidae). Appl. Entomol.
347 Zool. 37, 425-429. <https://doi.org/10.1303/aez.2002.425>
- 348 Oku, K., Yano, S., Takafuji, A., 2003. Different maternal effect on diapause induction of tetranychid
349 mites, *Tetranychus urticae* and *T. kanzawai* (Acari: Tetranychidae) Appl. Entomol. Zool. 38,
350 267-270. <https://doi.org/10.1303/aez.2003.267>
- 351 Oku, K., Yano, S., Takafuji, A., 2004. Nonlethal indirect effects of a native predatory mite,
352 *Amblyseius womersleyi* Schicha (Acari: Phytoseiidae), on the phytophagous mite *Tetranychus*
353 *kanzawai* Kishida (Acari: Tetranychidae). J. Ethol. 22, 109–112.
354 <https://doi.org/10.1007/s10164-003-0102-2>
- 355 Oku, K., Yano, S., 2007. Spider mite (Acari: Tetranychidae) deform their host plant leaves: an
356 investigation from the viewpoint of predator avoidance. Ann. Entomol. Soc. Am. 100, 69–72.
357 [https://doi.org/10.1603/0013-8746\(2007\)100\[69:SMATDT\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2007)100[69:SMATDT]2.0.CO;2)
- 358 Otsuki, H., Yano, S., 2014a. Potential lethal and non-lethal effects of predators on dispersal of spider
359 mites. Exp. Appl. Acarol. 64, 265–275. <https://doi.org/10.1007/s10493-014-9824-9>
- 360 Otsuki, H., Yano, S., 2014b. Predation risk increases dispersal distance in prey. Naturwissenschaften
361 101, 513–516. <https://doi.org/10.1007/s00114-014-1181-3>
- 362 Otsuki, H., Yano, S., 2017. Within-patch oviposition site shifts by spider mites in response to prior
363 predation risks decrease predator patch exploitation. Ethology 123, 453-459. <https://doi.org/10.1111/eth.12615>
- 364

- 365 Sabelis, M. W., Bakker, F. M., 1992. How predatory mites cope with the web of their tetranychid
366 prey: a functional view on dorsal chaetotaxy in the Phytoseiidae. *Exp. Appl. Acarol.* 16, 203–225.
367 <https://doi.org/10.1007/BF01193804>
- 368 Saito, Y., 1983. The concept of “life types” in Tetranychinae. An attempt to classify the spinning
369 behaviour of Tetranychinae. *Acarologia* 24, 377–391.
- 370 Shiotsuka, K., Yano, S., 2012. Coincidental intraguild predation by caterpillars on spider mites. *Exp.*
371 *Appl. Acarol.* 56, 355–364. <https://doi.org/10.1007/s10493-012-9514-4>
- 372 Škaloudová, B., Zemek, R., Křivan, V., 2007. The effect of predation risk on an acarine system.
373 *Anim. Behav.* 74, 813–821. <https://doi.org/10.1016/j.anbehav.2007.02.005>
- 374 Tollrian, R., Harvell, C. D., (Eds.) 1999. *The Ecology and Evolution of Inducible Defenses.*
375 Princeton Univ. Press, Princeton.
- 376 Wickler, W., 1968. *Mimicry in plants and animals.* McGraw-Hill, New York.
- 377 Zhang, Z. Q., 2003. *Mites of Greenhouses: Identification, Biology and Control.* CABI Publishing,
378 Wallingford, UK.

379

380 Captions

381 **Fig. 1** Experimental setup used to investigate the stealthiness of predatory mites: within- (solid
382 arrow) and between-patch (dashed arrow) dispersals of adult spider mite females in response to
383 predator intrusion.

384

385 **Fig. 2** Experimental setup used to investigate the stealthiness of predatory mites: oviposition site of
386 spider mite females in response to predator eggs.

387

Fig. 3 The proportion of *T. kanzawai* females that dispersed (a) within and (b) between patches. C, PP, NC, and NW indicate the control, *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. $*P < 0.05$, $**P < 0.001$ (Fisher's exact test with the Holm–Bonferroni correction).

Fig. 4 The proportion of *T. kanzawai* females preyed upon by each predatory mite species. PP, NC, and NW indicate the *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. $*P < 0.05$, $**P < 0.01$, $***P < 0.0001$ (Fisher's exact test with the Holm–Bonferroni correction).

Fig. 5 The proportions of *T. kanzawai* eggs laid on webs in response to eggs of each predatory mite species. PP, NC, and NW indicate the *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. $*P < 0.05$, $***P < 0.0001$ (Steel–Dwass test).

Fig. 6 The proportions of *T. kanzawai* eggs laid on webs in response to untreated and washed predator eggs of (a) *P. persimilis* and (b) *N. womersleyi* (Mann–Whitney *U*-test).

Fig. 7 The proportions of eggs laid on webs by females of (a) European and (b) Japanese *T. urticae* populations in response to eggs of the predatory mite species. PP, NC, and NW indicate the *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. $**P < 0.001$, $***P < 0.0001$ (Steel–Dwass test).

Graphical abstract

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7