

ARTICLE

Animal Ecology

Tiny predators avoid herbivorous caterpillar traces to prevent accidental predation

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Funding information

Japan Society for the Promotion of
Science, Grant/Award Numbers:
JP24KJ1495, JP25K09122

Handling Editor: Robert R. Parmenter

Abstract

We report the first example of predators having a strategy to avoid accidental predation by herbivorous insects. The predatory mites *Neoseiulus womersleyi* and *Euseius sojaensis* are smaller than 0.5 mm and lay eggs on plant leaf surfaces; thus, their immobile eggs would be incidentally consumed along with leaves by voracious lepidopteran caterpillars. We experimentally demonstrated that eggs of both mite species were preyed upon by tested hawkmoth caterpillars (*Theretra oldenlandiae*, *Theretra japonica*) along with leaves. Therefore, the ability to avoid such accidental predation should confer a selective advantage to mites. We further demonstrated that adult females of both mite species avoided laying eggs on leaves with traces of all tested caterpillars (*T. oldenlandiae*, *T. japonica*, *Papilio xuthus*, and *Bombyx mori*), indicating that eggs may avoid accidental predation by voracious caterpillars that may be nearby. This is the first demonstration of a repellent effect of herbivorous insect traces on carnivores. Considering previous studies showing that spider mites as small as predatory mites also avoid caterpillar traces, the same need to avoid predation by huge caterpillars may have led to the development of the same solutions for both spider mites and predatory mites.

KEYWORDS

accidental predation, caterpillar, Phytoseiidae, predation avoidance, predatory mite, trace

INTRODUCTION

Since some tiny herbivores can be subject to intraguild predation (IGP) when they are incidentally consumed by large herbivores along with shared host plants, they have developed strategies to avoid it (Gish et al., 2010; Kinto et al., 2023). Tiny herbivores experience IGP because they cannot immediately evacuate while large herbivores feed on leaves, and likewise, tiny predators that prey upon them are also likely to become involved in such predation. Therefore, the ability to avoid such accidental

predation should also confer a selective advantage to tiny predators. It has been reported that some predators can be killed by counterattacks by herbivores (Choh et al., 2012; Ono et al., 1995; Saitō, 1986) and hence some of these predators have strategies to avoid it (Faraji et al., 2001, 2002; Magalhães et al., 2005). However, there are few reports on predators avoiding one-sided “attacks” by large herbivores (Ben-Ari & Inbar, 2013; Berman & Inbar, 2023).

The predatory mites *Neoseiulus womersleyi* Schicha and *Euseius sojaensis* Ehara are typically <0.4 mm in

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size. The former is a specialist predator which preys only upon spider mites and the latter is a generalist predator which feeds on spider mites as well as non-prey resources such as pollen and pearl bodies. These mites may lay eggs on leaf hairs and in domatia of plant leaves infested by spider mites (Romero & Benson, 2005; Walter, 1996).

Lepidopteran larvae (hereafter “caterpillars”) such as *Theretra oldenlandiae* Fabricius and *Papilio xuthus* L. share food plants with spider mites that are preyed upon by predatory mites (Gerson, 2003; Mutuura & Issiki, 1965; van de Vrie et al., 1972). These caterpillars grow to 30–100 mm and consume food leaves along with the spider mites (Shirotsuka & Yano, 2012). For example, a final instar *T. oldenlandiae* consumes approximately 20 leaflets of *Cayratia japonica* (Thunb.) Gagnep. per day (Kinto et al., 2023).

Adult predatory mites can run fast and can escape quickly when a leaf-eating caterpillar approaches, while their eggs laid on the leaves cannot escape. Therefore, any behavior of a predatory mite that prevents its eggs from encountering caterpillars should confer a selective advantage to the mites. Since some predatory mite species exhibit the ability to detect their prey spider mite traces (Hislop & Prokopy, 1981; Shinmen et al., 2010; Yano & Osakabe, 2009), we hypothesized that egg-laying female predatory mites may avoid caterpillar traces, which signal ongoing caterpillar activity. Here, we provide the first report of caterpillars predating the eggs of predatory mites and predatory mites avoiding traces of herbivorous caterpillars.

MATERIALS AND METHODS

All the materials followed relevant institutional and national guidelines and legislation.

Predatory mites

We collected *E. sojaensis* individuals from kudzu vines, *Pueraria lobata* (Willd) Ohwi, in 2011 in Kyoto and reared them on tea pollen on expanded primary leaves of the kidney bean, *Phaseolus vulgaris* L. The leaf was pressed onto water-saturated cotton wool in Petri dishes (90 mm diameter, 14 mm deep; hereafter referred to as “leaf disc”). Water-saturated cotton wool served as a barrier to prevent mites from escaping. The Petri dishes were placed in transparent plastic containers and reared at a constant temperature of 25°C, 50% relative humidity, and 16:8 light:dark photoperiod (hereafter described as “laboratory conditions”).

The *N. womersleyi* individuals were collected from bushkiller plants (*C. japonica*) in 2015 in Kyoto and

maintained on leaf discs, which were heavily infested with *Tetranychus urticae* Koch as prey (30–50 female adults and individuals of other stages per leaf).

Herbivorous caterpillars

We used caterpillars of four lepidopteran species: *Theretra japonica*, *T. oldenlandiae*, *P. xuthus*, and *Bombyx mori* L. We collected eggs and larvae of *T. japonica* and *T. oldenlandiae* from *C. japonica* in 2022 in Kyoto, Japan, and reared them on *C. japonica* leaves until pupation. We collected eggs and larvae of *P. xuthus* from *Poncirus trifoliata* L. in 2022 in Kyoto, Japan, and reared them on *Citrus unshiu* Markovich leaves until pupation for only one generation. We obtained populations of the *B. mori* w1-pnd strain (Kyoto Inst. of Tech., Kyoto, Japan). We reared *B. mori* larvae on an artificial diet produced at the Kyoto Institute of Technology. We collected *N. womersleyi* individuals from *C. japonica*, the host plant of *T. japonica* and *T. oldenlandiae*. Furthermore, it has been reported that *E. sojaensis* uses the pearl bodies of *C. japonica* as alternative food (Ozawa & Yano, 2009). In addition, both predatory mite species are known to feed on *Panonychus citri* McGregor, which primarily feeds on citrus plants including *P. trifoliata* and *C. unshiu*, the host plants of *P. xuthus* (Kitashima & Gotoh, 1995; Nguyen & Shih, 2010). Therefore, the three caterpillar species (*T. japonica*, *T. oldenlandiae*, and *P. xuthus*) are likely to encounter the two predatory mite species in nature. In contrast, the *B. mori* strain is unlikely to encounter these predatory mites in nature because the strain has been domesticated for hundreds of years.

We reared caterpillars of *T. japonica*, *T. oldenlandiae*, and *P. xuthus* in 900 mL transparent plastic cups and caterpillars of *B. mori* in transparent plastic containers (140 × 220 × 35 mm). All caterpillars were maintained under laboratory conditions.

Plants

In the following tests, we used expanded leaflets of *C. japonica* for both hornworm species, and expanded primary leaves of *P. vulgaris* for *P. xuthus* and *B. mori*. Although the latter two caterpillars do not feed on *P. vulgaris*, we used the plant because leaves of original food plants (i.e., rutaceous and mulberry) have a more undulating morphology than *P. vulgaris* leaves, and when two leaf fragments are placed side by side in the following experiments, a step between the leaf fragments makes it difficult for small predatory mites to move through. *C. japonica* is a common perennial vine that reproduces

via both seed production and vegetative reproduction. We collected *C. japonica* leaves on the campus of Kyoto University. Leaf collection complied with local regulations and no permits were required.

Do caterpillars consume predatory mite eggs together with food leaves?

To examine whether caterpillars consume predatory mite eggs together with food leaves, we cut 20 × 20 mm leaf squares from *C. japonica* leaflets and placed them on water-saturated cotton. We then introduced two mated adult females of *E. sojaensis* or *N. womersleyi* onto each leaf square and maintained the setup under laboratory conditions. After 24 h, when the mites had laid an egg on the leaf square, we introduced the leaf square and a fifth instar hornworm (*T. japonica* or *T. oldenlandiae*) in a 200 mL transparent plastic cup. The caterpillars had previously been starved by isolation for more than 3 h. We repeated the procedure 50 times using 13 *T. japonica* individuals and 65 times using 11 *T. oldenlandiae* individuals, respectively. To ensure that tested caterpillars have the same level of hunger, we used each individual only once per day and we starved them before each test. Each leaf square and predatory mites were used only once.

Oviposition avoidance of predatory mites against caterpillar traces

To examine whether predatory mites (*E. sojaensis* and *N. womersleyi*) avoid laying eggs on plant surfaces bearing caterpillar traces, we conducted dual-choice tests using paired adjacent leaf squares with and without caterpillar traces. We did not use whole plants because it was practically difficult to induce caterpillar traces thoroughly on whole plants. For two hornworm species (*T. japonica* and *T. oldenlandiae*), we cut a 10 × 20 mm leaf piece from a *C. japonica* leaf and then cut the piece into two equal squares (10 × 10 mm). To introduce caterpillar traces to one square, we arranged them on a separate piece of paper towel on water-saturated cotton. This procedure was necessary because the caterpillars used were larger than individual leaf squares. Then we placed a final instar caterpillar on the squares and induced the caterpillar to walk across every leaf square three times (Figure 1a). We carefully removed all caterpillar-produced silk threads from the squares to evaluate the repellent effects of caterpillar trace chemicals rather than the physical structure of the silk threads. To minimize cross-contamination of trace chemicals, we removed silk threads with a fine needle wiped clean with ethanol each time, taking care the needle

did not touch the leaves. Within 30 min, we arranged the square (trace +) to touch against the other square (trace −) on water-saturated cotton in a Petri dish (90 mm diameter, 14 mm deep). Subsequently, a 2- to 4-day-old mated adult female of *E. sojaensis* or *N. womersleyi* was introduced onto a pointed piece of Parafilm in contact with both leaf edges using a fine brush (Figure 1a). We recorded the number of eggs laid on each leaf square at 24 h after its introduction. Each female mite and pair of leaf squares were used only once. There were 31 replicates using traces of *T. japonica* and 18 of *T. oldenlandiae* for *E. sojaensis*, as well as 27 and 14, respectively, for *N. womersleyi*. For the other two caterpillar species (*P. xuthus* and *B. mori*), we used fully expanded primary kidney bean leaves for substrates. We prepared bean leaf squares with caterpillar traces in the same manner described above. Then we arranged the square (trace +) to lie in close proximity to the control square (trace −) and compared the avoidance response of predatory mite females in the same manner described above.

Oviposition avoidance of predatory mites on plant stems bearing *T. japonica* traces

To examine whether predatory mite females avoid laying eggs on plant stems bearing caterpillar traces, we used kidney bean main stems (Figure 1b). We did not use *C. japonica* stems because they exude a sticky liquid which prevented predatory mites from crossing stem joints described below. We cut 50 mm stems from the kidney bean and divided them into two equal 25 mm lengths. We induced *T. japonica* traces on one stem by having the final instar caterpillar walk from end to end three times. We then arranged the stem piece (trace +) to touch against the other piece (trace −) on water-saturated cotton in a Petri dish, and introduced a 2- to 4-day-old mated adult female of *E. sojaensis* or *N. womersleyi* onto a pointed piece of Parafilm in contact with both stem edges using a fine brush (Figure 1b). After 24 h, we recorded the number of eggs laid on each stem piece. Each female mite and each stem were used only once. There were 16 replicates for *E. sojaensis*, as well as 14 for *N. womersleyi*.

Data analyses

The numbers of eggs laid by predatory mites on each leaf square or on each stem piece were compared in pairs using a generalized linear model with Poisson distribution using the R ver. 4.2.2 (R Foundation for Statistical Computing, Vienna, Austria), with a common null hypothesis that the number of eggs laid on both plant parts are equal.

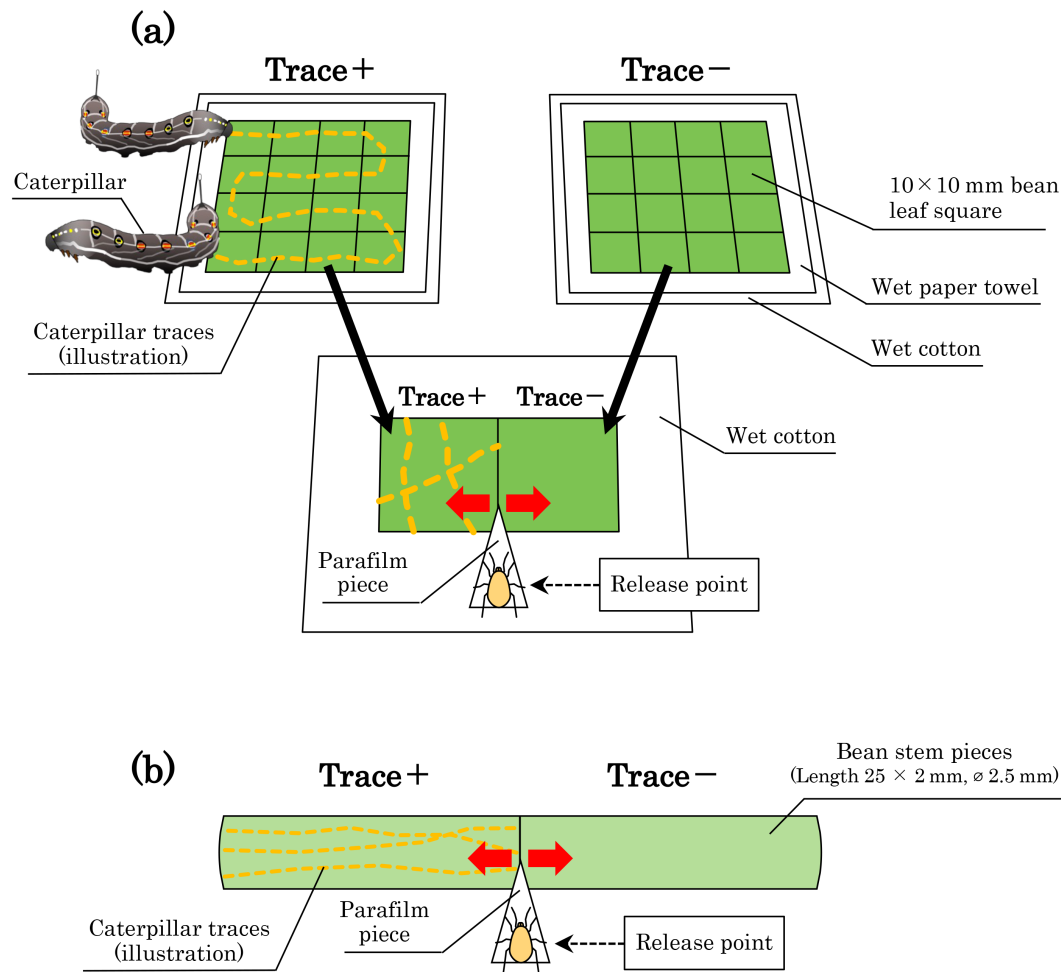


FIGURE 1 Procedures for observing the avoidance of caterpillar traces by predatory mites on (a) leaves and (b) stems. Illustration credit: S. Yano.

RESULTS

Do caterpillars consume predatory mite eggs together with food leaves?

All predatory mite eggs observed were consumed together with *C. japonica* leaves by both hornworms, indicating that hornworm caterpillars are not reluctant to consume predatory mite eggs. On the other hand, all predatory mite adults escaped safely from leaves either by stepping down from the leaves or by traveling over the body surface of the hornworms (Figure 2).

Oviposition avoidance of predatory mites against caterpillar traces

All *p* values shown below were obtained from GLMs (Poisson). *N. womersleyi* laid significantly fewer eggs on leaf squares bearing traces of *T. japonica* ($p < 0.0001$),

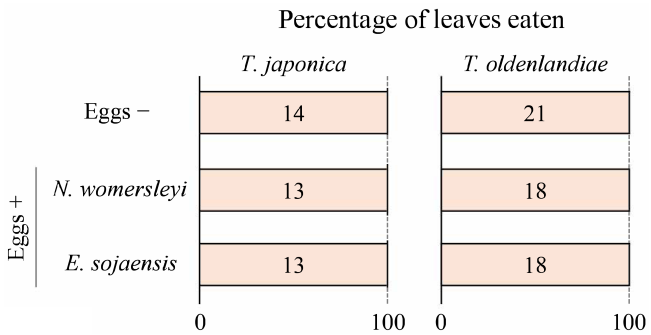


FIGURE 2 Proportion of *Cayratia japonica* leaves eaten by *Theretra japonica* or *Theretra oldenlandiae*. The numbers of leaf squares eaten by hawkmoth caterpillars are provided in each bar.

T. oldenlandiae ($p = 0.0100$), *B. mori* ($p < 0.0001$), and *P. xuthus* ($p = 0.0108$), as did *E. sojaensis* on leaf squares bearing traces of *T. japonica* ($p < 0.0001$), *T. oldenlandiae* ($p = 0.0007$), *B. mori* ($p < 0.0001$), and *P. xuthus* ($p = 0.0059$). This indicates that both predatory mites avoided laying eggs on leaves with hornworm traces (Figure 3a).

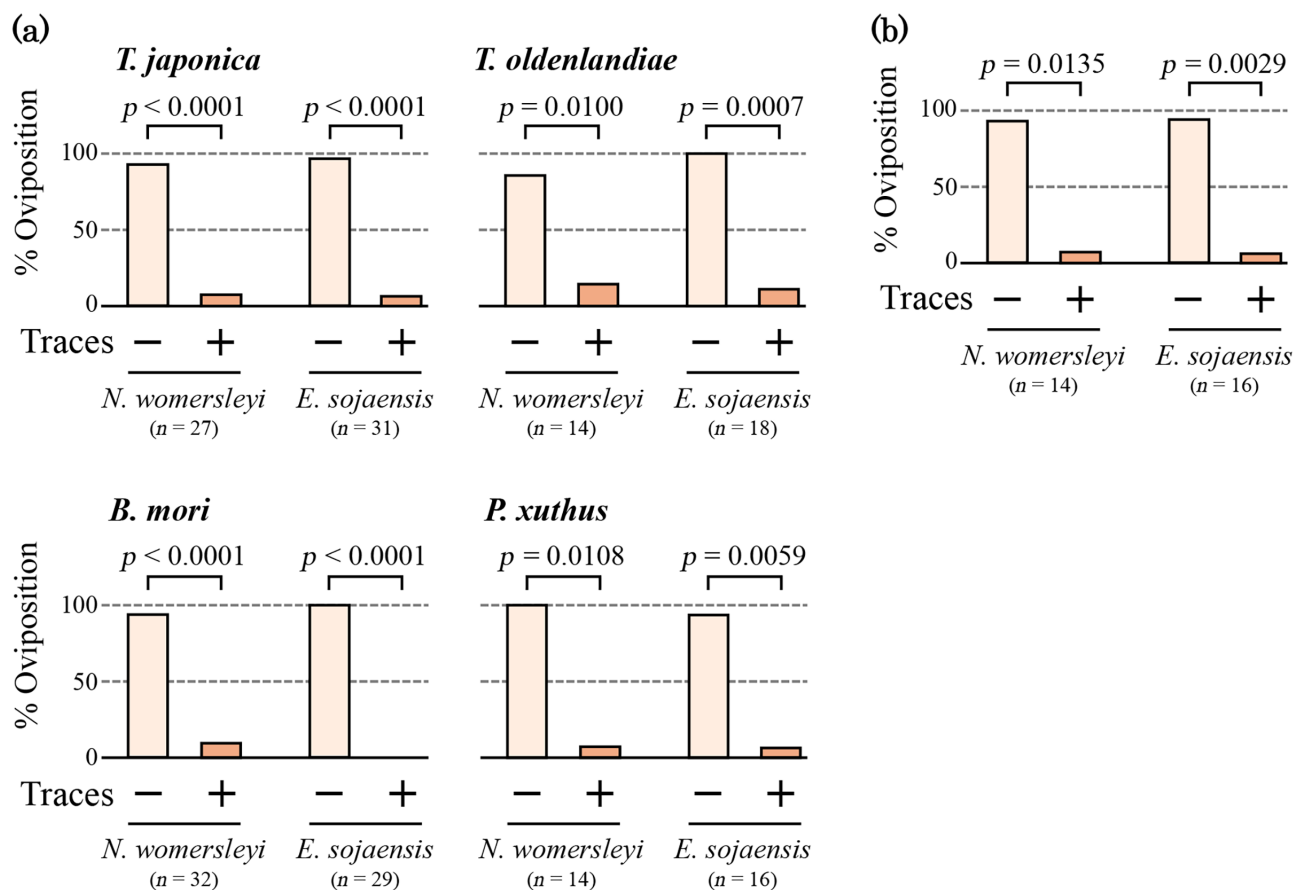


FIGURE 3 (a) Oviposition avoidance of predatory mites against caterpillar traces on leaves. (b) Oviposition avoidance of predatory mites against *Theretra japonica* traces on stems.

Oviposition avoidance of predatory mites on plant stems bearing *T. japonica* traces

Significantly fewer *N. womersleyi* ($p = 0.0135$, GLM, Poisson) and *E. sojaensis* ($p = 0.0029$, GLM, Poisson) females laid eggs onto kidney bean stems with *T. japonica* traces, indicating that both predatory mites avoided laying eggs on stems with traces of caterpillars (Figure 3b).

DISCUSSION

Herbivorous hawkmoth larvae incidentally fed on the eggs of predatory mites, but the mites never prey on huge hawkmoth larvae, so a trophic level reversal has occurred here. All eggs of both predatory mite species were eaten by both tested hawkmoth species along with food leaves, suggesting that predatory mites have no means of protecting their eggs from accidental predation by the approaching caterpillars. Encountering a final instar of hawkmoth, which consumes ca. 20 leaflets of *C. japonica* per day (Kinto et al., 2023), would pose a major threat to

the predatory mites. Both predatory mite species avoided laying eggs on plant leaves with traces of all tested caterpillar species. This avoidance will reduce the likelihood of accidental predation by voracious caterpillars that may be nearby. It would also prevent accidents where moving caterpillars crush predator eggs or cause them to fall from the plant. Avoidance by predatory mites of stems with caterpillar traces would contribute to reducing such accidents. This study is the first report to find that predators have strategies to avoid accidental predation by herbivorous insects.

Less mobile larvae of predatory mites are vulnerable to IGP and cannibalism (Hatherly et al., 2005; Maleknia et al., 2016; Schausberger, 2003); therefore, they can prevent such predation by taking refuge in leaf structures (e.g., domatia, pubescence), and spider mite webs (Ferreira, 2008, 2011; Prado et al., 2015; Roda et al., 2000; Seelmann et al., 2007). Moreover, female adults protect their eggs from such predation by avoiding oviposition in patches shared with such intraguild predators, and by watching over unhatched eggs (Saitoh et al., 2021; Walzer & Schausberger, 2012). However, these predation avoidance strategies are likely meaningless against

voracious caterpillars, which can consume an entire leaf within 10 min (Kinto et al., 2023). Because herbivore-induced plant volatiles emitted from caterpillar-infested plants may attract predatory mites and thereby increase the risk of accidental predation, avoidance of caterpillar traces would likely be even more adaptive.

We previously reported that spider mites as small as the predatory mites avoid the chemical components of these caterpillars' traces (Kinto et al., 2023). In this study, all silk threads produced by the caterpillars were removed prior to testing, so it is likely that the trace effects of the caterpillars are not mediated by silk threads but by trace chemicals, which will need to be verified in the future. Furthermore, both predatory mite species avoided not only the traces of caterpillar species encountered in nature but also those not encountered in nature, suggesting that the trace substances are likely common to many caterpillar species.

The importance of accidental predation due to predator–prey size differences has been largely ignored in ecological studies (Ben-Ari & Inbar, 2013; Berman & Inbar, 2023; Gish et al., 2010), but may be one of the major forces influencing habitat use by tiny animals regardless of their trophic levels. The avoidance of caterpillar traces by both spider mites and predatory mites may reflect the same need that led to the same solution of trace avoidance.

In an applied context, it is not necessarily a disadvantage that biological control agents for spider mites (predatory mite) avoid caterpillar traces as spider mites do. A previous study has shown that when UV-B irradiation and predatory mites are used together for spider mite control in a greenhouse, a synergistic effect is created because both spider mites and predatory mites avoid UV-B irradiation, making it easier for them to encounter in places on plants where UV-B irradiation cannot reach (Tanaka et al., 2024). Similarly, if there are caterpillar traces or their chemical components on the plant, spider mites and their biological control agents that avoid them are more likely to be encountered in places free of traces and their chemicals.

Identifying the chemical substances of caterpillar traces that predatory mites avoid is a key challenge for future research. It is also necessary to investigate whether caterpillar traces interfere with the effectiveness of predatory mites, which are biological control agents for spider mites in agricultural fields.

AUTHOR CONTRIBUTIONS

Shiori Kinto and Shuichi Yano conceived and designed experiments. Shiori Kinto conducted experiments and analyzed data. Shiori Kinto and Shuichi Yano wrote the manuscript.

ACKNOWLEDGMENTS

We would like to express our deepest appreciation to Y. Teramoto of Kyoto University and Drs. T. Akino and S. Nagaoka of Kyoto Institute of Technology for generously providing us with the animals and the artificial diet. We also thank A. Tanino and Dr. N. Hinomoto of Kyoto University who gave us valuable advice and encouragement. This work was supported by Japan Society for the Promotion of Science grant numbers JP24KJ1495 and JP25K09122.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kinto, 2025) are available from Figshare: <https://doi.org/10.6084/m9.figshare.30550790.v1>.

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How to cite this article: Kinto, Shiori, and Shuichi Yano. 2026. "Tiny Predators Avoid Herbivorous Caterpillar Traces to Prevent Accidental Predation." *Ecosphere* 17(4): e70627. <https://doi.org/10.1002/ecs2.70627>