Why does the predatory mite *Neoseiulus womersleyi* Schicha (Acari: Phytoseiidae) prefer spider mite eggs to adults?

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**Abstract**

Adult female *Neoseiulus womersleyi* feed on all stages of tetranychid mites, although they show a strong preference for eggs over adult females when both are available. We found that the oviposition rate of *N. womersleyi* females supplied with eggs of *Tetranychus kanzawai* or *T. urticae* was significantly higher than that of *N. womersleyi* females supplied with adult females of the respective prey species. The results suggested that the preference of *N. womersleyi* females for spider mite eggs simply reflected the optimal foraging of the females.

**Key words:** Prey preference; *Neoseiulus womersleyi*; *Tetranychus kanzawai*; *Tetranychus urticae*

**INTRODUCTION**

Although phytoseiid mites feed on all stages of tetranychid mites, many species have a strong preference for eggs over adult females when both are available (e.g., Takafuji and Chant, 1976; Fernando and Hassell, 1980; Blackwood et al., 2001). However, which of the spider mite eggs and adult spider mite females is an optimal diet (e.g., Charnov, 1976) for predatory mites has never been strictly compared. This may be because of the difficulty in measuring a fitness index of predatory mites supplied only with adult spider mite females that are constantly laying eggs.

The reproductive systems of predatory phytoseiid mites are generally pseudo-arhenotokous. Females mate before they disperse (Sabelis, 1985), and a single female can found a new population consisting of close relatives. *Neoseiulus womersleyi* persists on wild plants (e.g., Ehara and Shinkaji, 1996) where spider mites are patchily distributed and are not always abundant. Although adult female *N. womersleyi* can feed on both spider mite eggs and adult spider mite females (Furuichi, unpublished; also see Results), *N. womersleyi* larvae and protonymphs have difficulty in feeding on adult female tetranychid mites (Furuichi, unpublished). Therefore, these ecological conditions may have favored “prudent” *N. womersleyi* females that ensure a local prey supply by preserving adult spider mite females as a source of egg production.

If *N. womersleyi* females that feed only on adult spider mite females are as fit or fitter than those that feed only on eggs, then the preference of *N. womersleyi* females for eggs may be interpreted as an altruistic behavior at the cost of individual fitness. Otherwise, if *N. womersleyi* females that feed only on adult spider mite females are less fit than those that feed only on eggs, the preference of *N. womersleyi* females for eggs may simply reflect the optimal foraging of the female individuals.

In this study, we devised a new method to measure the fitness of predatory mites supplied with either adults or eggs of spider mites, and examined which of the above two hypotheses is plausible to explain the preference of *N. womersleyi* females for spider mite eggs.

**MATERIALS AND METHODS**

**Mites.** The closely related species *Tetranychus urticae* Koch and *T. kanzawai* Kishida feed on various host plant species and are considered important agricultural pests in Japan (e.g., Ehara and Shinkaji, 1996). *Tetranychus urticae* generally does not occur on wild plants, whereas *T. kanzawai* per-
sists mainly on wild plants (e.g., Takafuji and Morishita, 2001) and is one of the main prey items of *N. womersleyi* in Japan (e.g., Ehara and Shinkaji, 1996). *Neoseiulus womersleyi* is distributed throughout Japan (Ehara et al., 1994); because of its high predatory and reproductive ability (Mori and Saito, 1979; Hamamura, 1983), *N. womersleyi* is considered a biological control agent of tetranychid mites (e.g., Ehara and Shinkaji, 1996).

The study populations of *T. kanzawai* and *T. urchicae* were collected from a strawberry garden in Kyoto, Japan in 1998, and maintained on kidney bean (*Phaseolus vulgaris*) leaves placed on watersaturated cotton in Petri dishes (90 mm in diameter, 14 mm deep, hereafter referred to as ‘leaf disc’). *Neoseiulus womersleyi* was also collected in Kyoto in 1998, and reared on bean leaf discs that were heavily infested with *T. urchicae* as prey (30–50 adult females and individuals of other stages per leaf). All of the discs were placed together in a transparent plastic container and kept at 25°C and 50% relative humidity, with a photoperiod of L16 : D8 (hereafter referred to as ‘laboratory conditions’).

**Experimental arena.** To confine *N. womersleyi* on a resource patch, we used 20×20-mm bean leaf squares. We placed each square on a 15×15-mm absorbent piece of cotton fixed onto a thumbtack pasted in the center of a Petri dish. We then filled the Petri dish with water and adjusted the water level to the leaf surface (Fig. 1).

**Preference of *N. womersleyi* for eggs vs. adult female spider mites.** Using the arenas described above, we tested feeding preferences of the predatory mite for eggs and adult female spider mites. An objective of this experiment was not to compare food quality of the two prey types but to examine preference of the predatory mite for the two prey types that are likely to differ in encounter rate. To prevent female spider mites from ovipositing during the observations, we preliminarily confirmed that *T. kanzawai* and *T. urchicae* females did not lay eggs within 24 h after adult emergence under laboratory conditions.

We randomly selected mated adult female (2–5 d old) *T. kanzawai* and *T. urchicae* from the stock cultures. We introduced eight *T. kanzawai* females into each of 20 arenas. We also introduced six *T. urchicae* females into each of 20 additional arenas. The number of introduced females differed between species to adjust for the approximate total numbers of eggs per arena, as *T. urchicae* females lay more eggs than *T. kanzawai*. All arenas were kept under laboratory conditions. After 24 h, we removed the females and removed the eggs laid in excess of 30 in each arena. We obtained dozens of newly emerged females at the same time in the following manner. One day before an experiment, we introduced more than 200 teleiochrysalis females onto a 40×40-mm square of Parafilm ‘M’ (American National Can) placed onto water-saturated cotton in a Petri dish. The dish was covered with a transparent plastic lid to raise the relative humidity on the square and was held under laboratory conditions. At high relative humidity, tetranychid mites in the quiescent stages delay molting (Ikegami et al., 2000). After 24 h, the lid was removed. Nearly all females emerged within 30 min after the dish was uncovered. Newly emerged females were obtained in this manner.

We introduced eight newly emerged females into each arena and then introduced one adult *N. womersleyi* female (3–5 d old). Thus, the number of the two prey types was different on each arena; 30 eggs and eight adult spider mites. Based on the functional responses of *N. womersleyi*, the number of either prey types suffices for daily consumption of this phytoseiid mite (Hamamura, 1983). Moreover, adult female spider mites take refuge on webs in the presence of predatory mites (Oku et al., 2004), although they never counterattack against the predators. Therefore, the number of eggs and
adult female spider mites encountered by *Neoseiulus womersleyi* females per unit time may be different, which should be reflected on their feeding preference. After 16 h, we recorded the number of eggs and adults consumed. *Neoseiulus womersleyi* females that escaped from the arenas within 16 h were excluded from the data analysis.

**Performance of *Neoseiulus womersleyi* fed eggs or adult spider mites.** Preliminary observations indicated that *Neoseiulus womersleyi* females readily dispersed from uninfested arenas, while they settled in infested ones. To ensure settlement, we introduced eight newly emerged adult females of either *T. kanzawai* or *T. urticae* into each arena before the test and removed them after 1 d. In this manner, female spider mites were allowed to infest the arenas without laying eggs. We then introduced another eight newly emerged adult females of either species into each arena. We used 40 replicates for each species (adult group).

To provide *Neoseiulus womersleyi* with only spider mite eggs, we prepared 40 arenas with eight mated females (2–4 d old) of *T. kanzawai* or *T. urticae*. The spider mite females were allowed to oviposit for 1 d before they were removed. Each arena contained >30 eggs (egg group). We then introduced one mated female *Neoseiulus womersleyi* (3–5 d old) into each of the arenas and maintained them under laboratory conditions. As mentioned above, the number of prey encountered by *Neoseiulus womersleyi* females per unit time may be different between adult and egg groups. After 24 h, we transferred the *Neoseiulus womersleyi* to newly prepared arenas supplied with prey, in the manner described above. As a fitness index of *Neoseiulus womersleyi*, we recorded the number of eggs per arena laid on the second day. This was to exclude possible effects of previous feeding by *Neoseiulus womersleyi*. We also recorded the number of eggs and female spider mites consumed. *Neoseiulus womersleyi* females that died or escaped from the arenas during the experiments were excluded from the data analysis. No individual *Neoseiulus womersleyi* was able to exhaust prey resources in an arena during this study.

In addition, we also measured the fitness index of *Neoseiulus womersleyi* feeding only on *T. kanzawai* females at the teleiochrysalis stage, i.e., immediately before the adult stage, which is similar to eggs in terms of accessibility (both are quiescent stages). We transferred ten young teleiochrysalis *T. kanza-

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**RESULTS AND DISCUSSION**

In the experiment testing the prey preference of *Neoseiulus womersleyi*, although the numbers of the two preys were different on each arena (30 eggs and eight adults), *Neoseiulus womersleyi* females preferred eggs to adult female spider mites under these conditions. No *T. kanzawai* adults were consumed, while 12.44±1.61 (mean±SE; n=16) eggs were consumed. Similarly, 0.18±0.095 (mean±SE; n=17) *T. urticae* adults were consumed, while 12.18±2.64 (mean±SE; n=17) eggs were consumed.

*Neoseiulus womersleyi* females provided with *T. kanzawai* eggs consumed 14.56±1.01 (mean±SE; n=32) eggs and laid 1.88±0.11 (mean±SE; n=32) eggs, while *Neoseiulus womersleyi* females feeding on *T. kanzawai* adults consumed 1.71±0.20 (mean±SE; n=28) adults and laid 1.18±0.10 (mean±SE; n=28) eggs (Fig. 2a). Thus, *Neoseiulus womersleyi* females that fed on *T. kanzawai* eggs laid significantly more eggs than did those that fed on *T. kanzawai* adults (p<0.0001, Mann-Whitney U-test). Similarly, *Neoseiulus womersleyi* females feeding on *T. urticae* eggs consumed 25.40±2.49 (mean±SE; n=30) eggs and laid 2.50±0.14 (mean±SE; n=30) eggs, while *Neoseiulus womersleyi* females feeding on *T. urticae* adults consumed 3.48±0.33 (mean±SE; n=31) adults and laid 1.58±0.19 (mean±SE; n=31) eggs. The number of eggs laid by *Neoseiulus womersleyi* differed significantly between the groups (p<0.0001, Mann-Whitney U-test; Fig. 2b).

Our results clearly showed that for both prey species examined, the fitness index of *Neoseiulus womersleyi* females supplied with eggs was significantly higher than that of females supplied with adult spider mites. Therefore, the preference of *Neoseiulus womersleyi* females for spider mite eggs over adults may simply reflect the individual fitness of *Neoseiulus womersleyi* females.

Another important concern is the proximate reason why the fitness index of *Neoseiulus womersleyi* females
was lower when they were supplied with adult spider mites only. It is possible that quiescent eggs are more accessible than active female adults, who take refuge on webs in the presence of predators (Oku et al., 2004). To test this hypothesis, we supplied a group of adult *N. womersleyi* females with *T. kanzawai* females at the teleiochrysalis stage, i.e., the quiescent stage immediately before adult emergence. This experiment revealed that both teleiochrysalis and adult *T. kanzawai* females were equally unsuitable for *N. womersleyi* as prey compared to eggs (Fig. 2a). Therefore, it is likely that the low fitness index of *N. womersleyi* females feeding on adult *T. kanzawai* females was not attributed to the low accessibility of the prey. Rather, it may be due to lower nutritional benefits or higher handling costs compared to those associated with the eggs. However, it is possible that food quality of teleiochrysalis females was lower than that of adult females, owing to thick wax for example, and it may have exactly offset the benefit of higher accessibility of teleiochrysalis females compared with adult females. This possibility remains to be clarified in future studies.

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