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5 Effects of combination between web density and size of spider mite on predation by a generalist and a
6 specialist phytoseiid mite
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14

15 **Abstract**

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17 Complicated three-dimensional webs of silk threads produced by *Tetranychus* spider mites provide
18 protection from predation by many generalist phytoseiid mite species. Accessibility to prey may be
19 the most significant criterion for successful predation in complicated webs. To assess the
20 protective effects of combination between web size and density, we compared predation on eggs of the
21 two-spotted spider mite, *Tetranychus urticae*, by a generalist (*Euseius sojaensis*) and a specialist
22 (*Neoseiulus womersleyi*) phytoseiid mite in the laboratory under manipulated web size and density. Web
23 sizes negatively affected to the predation. Significant interactions were found between phytoseiid mite
24 species and prey distribution; egg consumption by *E. sojaensis* was more in uniform distribution, but that
25 by *N. womersleyi*, in contrast, was larger in contagious distribution. However, the egg consumption by *E.*
26 *sojaensis* and *N. womersleyi* were both mitigated in larger webs. This area size depending mitigation was
27 more effective to the predation by *E. sojaensis*. Although the mechanism of web size depending
28 mitigation is unknown, web sizes might affect prey searching efficiency of this phytoseiid mite.
29 Consequently, combination between web density and size are likely to affect not only a generalist *E.*
30 *sojaensis* but also a specialist *N. womersleyi*.

31

32 **Keywords:** Web size, Web density, *Euseius sojaensis*, *Neoseiulus womersleyi*, Tetranychidae,
33 Phytoseiidae

34

35 **Introduction**

36

37 *Tetranychus* spider mites (Acari: Tetranychidae) produce complicated three-dimensional silk webs,
38 on which they deposit eggs, fecal pellets, and cast skins (Saito 1983). These webs provide refuge from
39 predation by generalist phytoseiid mites by impeding and entangling them (McMurtry and Scriven 1964,
40 McMurtry and Johnson 1965, Osakabe 1988). *Tetranychus* spider mites usually spin silk threads as they
41 walk (Saito 1983). Therefore, larger groups of individuals construct denser, more complex webs that may
42 confer greater protection from generalist phytoseiid mites. However, webs also provide a prominent
43 prey-searching cue for specialist phytoseiid mites (Hislop and Prokopy 1981, Hoy and Smilanick 1981,
44 Sabelis et al. 1984, Furuichi et al. 2005, Yano and Osakabe 2009, Shinmen et al. 2010).

45 Accessibility to prey (i.e., capacity to penetrate complicated webs) may be the most significant
46 criterion for successful predation by phytoseiid mites in complicated webs produced by *Tetranychus*
47 spider mites (Sabelis and Bakker 1992, Shimoda et al. 2009). *Euseius sojaensis* Ehara (Acari:
48 Phytoseiidae) is a generalist phytoseiid mite (Type IV; McMurtry and Croft 1997) incapable of
49 penetrating complicated webs (Osakabe et al. 1986, 1987; Osakabe 1988). However, Ozawa and Yano
50 (2009) pointed out that although prey is inaccessible after the web is completely constructed, *E. sojaensis*
51 can prey on *Tetranychus* mites at the beginning of colonization. Moreover, Yano (2012) showed that
52 increasing the interval between the start of *Tetranychus* spider mite colonization and prey searching by *E.*
53 *sojaensis* significantly mitigated predation. Accumulation of webs during this interval may provide better
54 protection, whereas the protective function of sparse webs may be insufficient even against a generalist
55 phytoseiid mite. Although examinations of this relationship usually assume that spider mites and their
56 eggs are distributed throughout their webs, predation risk to eggs may be higher if those are distributed
57 near the web's edge. In this context, predation risk would be higher when the webbing area is smaller.
58 However, the protective effects of combination between web density and size have not been addressed
59 virtually.

60 To assess the protective effects of combination between web size and density, we compared predation
61 on eggs of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), by *E. sojaensis*
62 and *Neoseiulus womersleyi* (Schicha) (Acari: Phytoseiidae) in the laboratory under manipulated webbing
63 area size and aggregation of adult females involving prey egg distribution and also web density in the area.

64 *Neoseiulus womersleyi* is a specialist phytoseiid mite native to Japan that prefers *Tetranychus* mites (Type
65 II; McMurtry and Croft 1997).

66

67 **Materials and methods**

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69 Mites

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71 *Neoseiulus womersleyi* were collected from roses (Rosaceae) in Nara, Japan and reared on *T. urticae* on
72 kidney bean, *Phaseolus vulgaris* L. (Leguminosae), leaves placed on water-soaked cotton in Petri dishes
73 (9 cm in diameter). *Euseius sojaensis* were collected from kudzu vines *Pueraria lobota* (Willd) Ohwi
74 (Leguminosae) in Kyoto and reared on tea pollen on plastic film (Parafilm, Pechiney Plastic Packaging
75 Co., IL; 5 cm in diameter) placed on water-soaked cotton in Petri dishes. A laboratory population of *T.*
76 *urticae* (the yellow-green type) from several different localities in Japan and cultured on potted kidney
77 bean plants has been established in our laboratory for more than 7 years. This was also reared on kidney
78 bean leaves on water-soaked cotton in Petri dishes for several generations before use in the experiments.

79 Petri dishes were placed in transparent plastic containers and kept at $25 \pm 2^\circ\text{C}$ and $50 \pm 5\%$ relative
80 humidity (RH), with a photoperiod of 16L8D. All experiments were conducted under the same conditions
81 as rearing. We used 2 to 3-day-old mated females of *T. urticae*, *N. womersleyi*, and *E. sojaensis* in all
82 experiments.

83

84 Experimental design

85

86 We prepared 10×10 -mm or 15×15 -mm leaf squares cut from kidney bean leaves, excluding the main
87 vein, as experimental patches. We pressed four (10 mm) or two (15 mm) leaf squares onto water soaked
88 cotton in each Petri dish (9 cm in diameter). We put two wet cotton threads on each leaf square to divide it
89 into four experimental quadrats. Four *T. urticae* females were then introduced individually into each
90 quadrat (uniform distribution; Fig. 1a) or together into one quadrat (contagious distribution; Fig. 1b) in a
91 leaf square.

92 After 24 h, we recorded the number of eggs laid in each quadrat; then, we carefully removed females

93 and wet cotton threads so as not to destroy the webs. An adult female of *E. sojaensis* or *N. womersleyi*
94 was introduced at the center of each leaf square. To ensure they were in a uniformly starved condition, the
95 phytoseiid mites were kept individually in 1.5-ml sample tubes with a water droplet for 48 h before the
96 experiments. After 24 h, we recorded the number of *T. urticae* eggs consumed. If a phytoseiid mite
97 escaped from the leaf square during an experiment, the data were excluded from the following analyses.

98 The area covered by complicated webs was in direct proportion to the area walked by *T. urticae*
99 females, which ranged from 50 to 100 mm² over 10–90 min in a laboratory experiment by Saito (1977).
100 In our experiments, *T. urticae* adult females were allowed to walk freely in a 25-mm² (in the case of the
101 10-mm square) or 56.25-mm² (15-mm square) quadrat for 24 h. Therefore, quadrat sizes roughly
102 corresponded to the area of complicated webs produced by *T. urticae*.

103 Replications (leaf squares) of uniform and contagious distributions against *E. sojaensis* numbered 15
104 and 12, respectively, for 10-mm squares and 11 and 12, respectively, for 15-mm squares. Replications of
105 uniform and contagious distributions against *N. womersleyi* numbered 16 and 8, respectively, for 10-mm
106 squares, and 20 and 16, respectively, for 15-mm squares.

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108 Data analysis

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110 We compared the numbers of eggs deposited in leaf squares among square sizes and distributions of
111 introduced *T. urticae* females using a Wald test in a generalized linear model (GLM; Poisson error).
112 Effects of area sizes and distribution of prey eggs on egg consumption by phytoseiid mites were analyzed
113 using a linear model. Prior to this analysis, proportion of eggs consumed by phytoseiid mites were
114 transformed to empirical logit. All analyses were conducted in R v. 2.15.2 (R Core Development Team
115 2012).

116

117 **Results**

118

119 The number of eggs produced by four *T. urticae* females ranged from 42 to 56 (Table 1), and more on
120 15-mm than on 10-mm squares (Table 2 A). The distribution pattern of *T. urticae* females also
121 significantly affected egg production: more in uniform than contagious distribution (Table 2 D).

122 No significant difference was detected in prey egg consumption between phytoseiid mite species
123 (Table 3 P). Whereas, the area sizes negatively affected to the predation; egg predation rate was larger on
124 10-mm leaf squares than 15-mm leaf squares (Fig. 2, Table 3 A), and this trend was clear in *E. sojaensis*
125 in comparison with *N. womersleyi* (Table 3 P×A). Effects of prey distribution on egg consumption were
126 marginal (Table 3 D). However, egg consumption by *E. sojaensis* decreased in contagious distribution of
127 prey in comparison with uniform distribution on 10-mm leaf squares, but that by *N. womersleyi*, in
128 contrast, increased in contagious distribution (Fig. 2, Table 3 P×D). No interaction was detected between
129 leaf size and distribution of prey eggs (Table 3 A×D).

130

131 **Discussion**

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133 The egg consumption rates demonstrate opposite effects of aggregation of prey eggs to predation by *E.*
134 *sojaensis* and *N. womersleyi* in smaller area (10-mm squares). Contagious distribution decreased
135 predation by *E. sojaensis*, indicating that dense webs produced by aggregated females increased
136 protection effects. This may reflect weakness of *E. sojaensis* to complicated webs of *Tetranychus* mites
137 (Osakabe et al. 1986, 1987; Osakabe 1988). In contrast, predation by *N. womersleyi* increased in
138 contagious distribution. Dense webs did not affect the degree of protection from predation by *N.*
139 *womersleyi*. Instead, the dense webs might be exploited as a prey-searching cue because this phytoseiid
140 mite follows *T. urticae* trail including threads (Yano and Osakabe 2009, Shinmen et al. 2010) and their
141 prey preference is strongly affected by spider mite webs (Fruichi et al. 2005). Moreover, the extent of *N.*
142 *womersleyi*'s prey consumption may be due to its ability to cut silken threads while moving within the
143 webs (Shimoda et al. 2010).

144 In contrast, predation risks by *E. sojaensis* in uniform distribution and by *N. womersleyi* in
145 contagious distribution were both mitigated in larger area (15-mm squares). This area size depending
146 mitigation was more effective to the predation by *E. sojaensis*. Denser webs conferred stronger protection
147 from predation by *E. sojaensis* on 10-mm leaf squares as described above. However, the web density was
148 lower on 15-mm than 10-mm leaf squares in the same distribution because webs were created by the same
149 number of individuals. This demonstrated that predation by *E. sojaensis* was affected by the combination
150 between web density and size. Interestingly, egg consumption by *N. womersleyi* in contagious distribution

151 also decreased in 15-mm leaf squares. Although the mechanism of this phenomenon is unknown, web
152 sizes might affect prey searching efficiency of this phytoseiid mite. Therefore, combination between web
153 density and size are likely to affect not only a generalist *E. sojaensis* but also a specialist *N. wormersleyi*.
154

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156

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209

210 Figure legend

211

212 Fig. 1 Design for uniform (a) and contagious (b) distribution treatment of *Tetranychus urticae* females
213 (solid circles) over four quadrats separated by wet cotton threads on kidney bean leaf squares
214 (10- or 15-mm square)

215

216 Fig. 2 Predation rates on uniformly and contagiously distributed prey eggs by *Euseius sojaensis* (A, B)
217 and *Neoseiulus womersleyi* (C, D) on 15-mm leaf squares (A, C) and 10-mm leaf squares (B, D)
218 for 24 h. Vertical lines at the top of bars represents standard errors (SE). The mean and SE values
219 were calculated with arc sin transformed predation rates of replications.

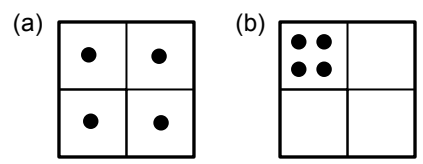


Fig. 1

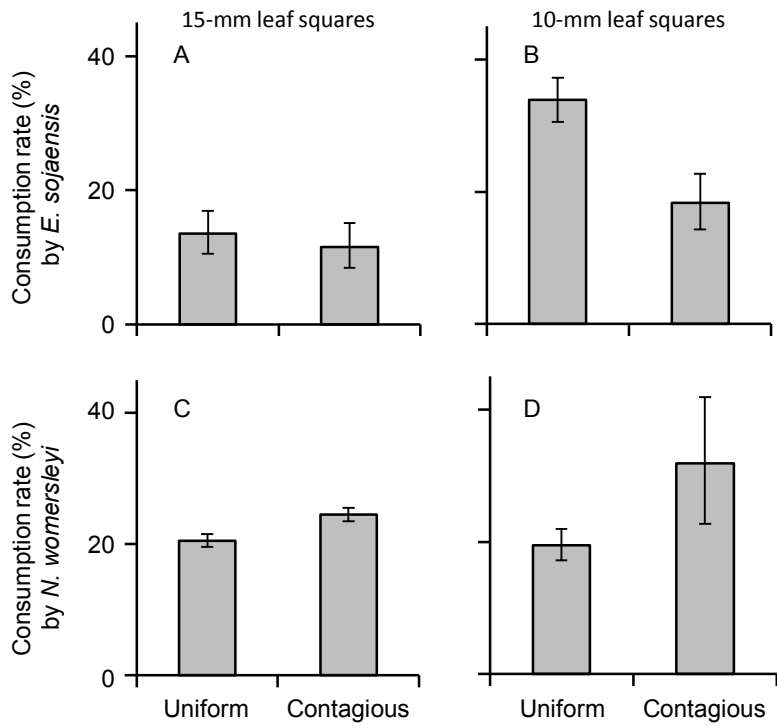


Fig. 2