1   **The stealthiness of predatory mites as spider mite biological control agents**

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10   **Abstract**

11   Adult spider mite females that are aware of predatory mites can reduce predation by dispersing from

12   patches invaded by predators or by shifting their oviposition site onto webs where eggs are predated

13   less than on leaf surfaces. Therefore, the stealthiness of predatory mites stalking spider mite females

14   should largely determine the success of spider mite control. This study examined the stealthiness of

15   three predatory mites: *Phytoseiulus persimilis* Athias-Henriot, *Neoseiulus californicus* McGregor,

16   and *Neoseiulus womersleyi* Schicha. The first two species have been commercialized as spider mite

17   biological control agents, whereas the last species is a native predator of spider mites in Japan. We

18   measured two indices of predator stealthiness in bioassays using *Tetranychus kanzawai* Kishida as

19   prey: the proportion of prey mites that dispersed from their patches in response to predator intrusion

20   and the proportions of prey eggs laid on webs in response to predator eggs. Both indices resulted in

21   the same ranking, with *P. persimilis* ranking highest and *N. womersleyi* lowest. The greater

22   stealthiness of *P. persimilis* eggs compared with *N. womersleyi* eggs seemed to be due to the lower

23   amount of detectable substances on the egg surface. We also measured this index of stealthiness for

24   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.

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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.

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57   The utility of predatory mites as spider mite biological control agents has conventionally

58   been evaluated using indices such as the predation rate and intrinsic rate of natural increase (*e.g.*,

59   Janssen and Sabelis, 1992, Gotoh et al., 2006). These indices are measured under laboratory

60   conditions where neither spider mites nor predatory mites have opportunities for dispersal. Under

61   such conditions, the predatory mites eventually consume all of the spider mites, even if the prey is

62   aware of the predators and tries to disperse from the patch. Therefore, the conventional indices may

63   fail to reflect possible differences in predator stealthiness to spider mites. Moreover, rearing

64   experimental animals under laboratory conditions usually deprives them of dispersal opportunities,

65   so we must always remember that we may observe artifacts under experimental conditions, *i.e.*,

66   behaviors of target experimental animals that would otherwise have dispersed from the patch.

67   To quantify predator stealthiness to spider mites, we measured the proportion of mated

68   female spider mites (*i.e.*, the dispersing stage) that dispersed from their webs in response to predator

69   intrusion using a setup allowing prey dispersal. We also measured the proportions of spider mite

70   eggs laid on webs in response to predatory mite eggs. We used *T. kanzawai* as the prey species, as

71   this species has been reported to disperse (Oku et al., 2004, Bowler et al., 2013) or shift oviposition

72   sites onto webs (Oku and Yano, 2007, Otsuki and Yano, 2017) in response to predatory mites. As

73   predatory mites, we examined two commercialized biological control agents used against spider

74   mites of the genus *Tetranychus*: *Phytoseiulus persimilis* (Hussey and Bravenboer, 1971) and

75   *Neosiulus californicus* (Cooping, 2001). We also examined *N. womersleyi*, which is a native

76   predator of *T. kanzawai* in Japan (Hamamura, 1986), but has not been commercialized as a

77   biological control agent. *Neoseiulus womersleyi* can invade *T. kanzawai* webs (Oku et al., 2004),

78   and can control *T. kanzawai* populations under certain conditions (Kondo, 2004). To examine

79   whether stealthiness is affected by the species and populations of spider mite used, we also

80   measured the anti-predator behaviors of European and Japanese populations of a related spider mite,

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81   *T. urticae*. Based on these results, we discuss whether the degree of stealthiness is consistent across

82   species and populations of prey mites.

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84   **2. Materials and Methods**

85   2.1 Mites

86   The *T. kanzawai* study population was collected in September 2014 in Kyoto, Japan, and was reared

87   on expanded primary leaves of kidney bean (*Phaseolus vulgaris* L.), which were cut from the petiole

88   and pressed onto water-saturated cotton in Petri dishes ("leaf discs"). The water-saturated cotton

89   served as a barrier to prevent the mites from escaping, and all experimental setups were placed on

90   water-saturated cotton. The leaf discs were placed in transparent plastic containers maintained at 25

91     $\pm$ 1°C, 50 $\pm$ 1% relative humidity, and a 16L (7:00–23:00):8D photoperiod. All experiments were

92   conducted under these laboratory conditions. The study populations of *T. urticae* were collected in

93   2008–2009 in the northern Netherlands (European population, Khajehali et al., 2011) and in 1998 in

94   Nara, Japan (Japanese population). These populations were maintained in the manner described

95   above.

96   We obtained a population of *P. persimilis* from a commercial source in Europe (Koppert Biological

97   Systems, The Netherlands), and maintained the population for more than 10 years on kidney bean

98   (*Phaseolus vulgaris*) leaf discs that were heavily infested with *T. urticae* (Japanese population) as

99   prey. Therefore, the population should not have a coevolutionary history with *T. kanzawai*, which

100   occurs only in Asia (Ehara, 1999). The *N. californicus* study population was collected in 2000 in

101   Nagano, Japan, and that of *N. womersleyi* in 2014 in Kyoto, Japan. These populations were reared

102   on bean leaf discs in the same manner.

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104   2.2 Dispersal of *T. kanzawai* females in response to predator intrusion

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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-mm^2 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 (Bioramo

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-mm^2 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-mm^2 uninfested leaf square (trap) by a non-food substrate (30×10-mm^2 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

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129 days had elapsed. We considered a *T. kanzawai* female to have dispersed within the patch if an

130 uninfested area of the initial patch contained webs, injury scars, feces, and eggs, regardless of the

131 presence of the female, whereas we considered the female to have dispersed between patches if the

132 trap contained these signs. There were 39 replicates without a predator, 43 with *P. persimilis*, 45

133 with *N. californicus*, and 45 with *N. womersleyi*.

134   The proportion of *T. kanzawai* females that had dispersed from the bent leaf squares (both

135 within- and between-patch) in response to each predatory mite species was compared with the

136 control without a predator using Fisher's exact test. The proportion of *T. kanzawai* females preyed

137 upon during the experiment was compared among predatory mite species using Fisher's exact test.

138 The Holm–Bonferroni correction was used to adjust *P*-values for multiple comparisons. The

139 statistical analyses were performed using R v.3.2.2 (R Foundation for Statistical Computing, Vienna,

140 Austria).

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142 2.3 Oviposition site selection of spider mites in response to predator eggs

143 As another stealthiness index of predatory mites, we examined the proportions of spider mite eggs

144 laid on webs in response to predator eggs. We did not use adult predators in this experiment because

145 they consume spider mite eggs, making it impossible to calculate the proportion of eggs on the

146 webs.

147   Based on the method of Oku and Yano (2007), 10×10-mm^2 bean leaf squares were bent to

148 standardize the patch structure used for building spider mite webs (Fig. 2). Then, we obtained eggs

149 of the three predatory mite species within 24 h of oviposition and transferred three eggs of one

150 species onto the bottom of the bent leaf surfaces. Next, we introduced a mated *T. kanzawai* female 2

151 days after maturation onto the bent leaf. After 24 h, we counted the number of eggs laid on both the

152 leaf surface and the web. The proportions of *T. kanzawai* eggs laid on webs were compared among

153   the predatory mite species using the Steel–Dwass test. There were 42 replicates with *P. persimilis*

154   eggs, 38 with *N. californicus* eggs, and 41 with *N. womersleyi* eggs.

155   To examine whether concealing or detectable surface materials were responsible for the

156   different degrees of stealthiness, eggs of *P. persimilis* (least detectable, see Results) and *N.*

157   *womersleyi* (most detectable, see Results) were dipped in kitchen detergent (Kyukyutto; Kao,

158   Tokyo) diluted 10-fold with water. After 10 s, the eggs were rinsed with a fine brush in ample

159   distilled water for 10 s to remove the detergent from the eggs. Since the detergent is for dishwashing,

160   it should be completely removed by rinsing in water. We first confirmed that the treatment did not

161   have harmful effects on predatory mite eggs. The proportions of *T. kanzawai* eggs laid on webs in

162   response to three untreated or washed eggs of the respective predator species were measured in the

163   manner described above. We hypothesized that removing the surface materials would make the

164   washed *P. persimilis* eggs more detectable (resulting in more oviposition on webs) if the materials

165   served as concealment, whereas detectable surface materials should make the washed *N. womersleyi*

166   eggs less detectable (resulting in less oviposition on webs). The proportions were compared between

167   untreated and washed eggs using the Mann–Whitney *U*-test. There were 39 replicates with untreated

168   *P. persimilis* eggs, 37 with washed *P. persimilis* eggs, 38 with untreated *N. womersleyi* eggs, and 43

169   with washed *N. womersleyi* eggs.

170   To examine whether the stealthiness index is consistent across prey mites or is affected by

171   the species and origins of the prey populations used, we also examined the oviposition site pattern

172   using a related spider mite, *T. urticae*. Because the *P. persimilis* used originated from Europe, while

173   *N. californicus* and *N. womersleyi* are from Japan, we used European and Japanese populations of *T.*

174   *urticae* to examine this question. The proportions of eggs laid on webs were examined in the manner

175   described above and compared among predatory mite species for the various *T. urticae* populations

176   using the Steel–Dwass test. There were 36 replicates with *P. persimilis* eggs, 33 with *N. californicus*

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

178 35, respectively, for the Japanese *T. urticae* population.

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180 **3. Results**

181 3.1 Dispersal of *T. kanzawai* females in response to predator intrusion

182 The within-patch dispersal of *T. kanzawai* females in response to *P. persimilis* and *N. womersleyi*

183 did not significantly differ from that of the control without predators. Only within-patch dispersal in

184 response to *N. californicus* was significantly lower than that of the control (Fig. 3a). Between-patch

185 dispersal of *T. kanzawai* females in response to *P. persimilis* and *N. californicus* did not

186 significantly differ from that of the control, whereas between-patch dispersal in response to *N.*

187 *womersleyi* was significantly higher than that of the control (Fig. 3b). In addition, the proportion of

188 *T. kanzawai* females preyed upon by *P. persimilis* was the highest, while that by *N. womersleyi* was

189 the lowest. The differences were significant between all pairs of predatory mite species (Fig. 4).

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191 3.2 Oviposition site selection of spider mites in response to predator eggs

192 The proportions of *T. kanzawai* eggs laid on webs in response to *N. womersleyi* were the highest

193 (the least stealthy), while that in response to *P. persimilis* was the lowest (the greatest stealthiness).

194 Significant differences were found between all pairs of predatory mite species (Fig. 5).

195 The proportions of *T. kanzawai* eggs laid on webs in response to washed *P. persimilis* eggs

196 were slightly lower than that in response to untreated eggs (Fig. 6a), whereas those in response to

197 washed *N. womersleyi* eggs were considerably lower than that in response to untreated *N.*

198 *womersleyi* eggs (Fig. 6b). These results suggest the existence of detectable, rather than concealing,

199 surface materials on *N. womersleyi* eggs.

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200   The proportions of eggs deposited on webs by *T. urticae* females of European and Japanese

201   populations in response to predatory mite eggs showed the same pattern seen using *T. kanzawai*

202   females. Significant differences were found between all pairs, except for the *N. californicus* and *N.*

203   *womersleyi* pair examined with the European *T. urticae* population and the *P. persimilis* and *N.*

204   *californicus* pair examined with the Japanese *T. urticae* population (Fig. 7).

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206   **4. Discussion**

207   We systematically measured stealthiness indices of predatory mites, the proportion of prey mites

208   dispersed from their patches in response to predator intrusion, and the proportions of prey eggs laid

209   on webs in response to predator eggs in environments where predator-induced dispersal and

210   oviposition site shifts onto webs are possible. We found that both indices resulted in the same

211   ranking across prey species and prey populations, with *P. persimilis* ranking highest and *N.*

212   *womersleyi* lowest.

213   *Tetranychus kanzawai* females dispersed from patches intruded upon by *N. womersleyi*, but

214   did not disperse from patches intruded upon by *P. persimilis* or *N. californicus*. If this result was

215   due to the relatively low predation rate by *N. womersleyi*, compared to the other two predator

216   species (Fig.4), then we should have obtained the highest proportion of dispersed *T. kanzawai*

217   females in the absence of predation (*i.e.* control). In contrast, the proportion of *T. kanzawai* females

218   that dispersed from control patches did not differ from those in response to *P. persimilis* or *N.*

219   *californicus*. Therefore, we may reasonably conclude that *T. kanzawa*i females were less aware of *P.*

220   *persimilis* and *N. californicus* than of *N. womersleyi*, and hence more females were preyed upon by

221   the former two predator species. *Neoseiulus womersleyi* promoted the between-patch dispersal of

222   prey mites, which might in turn increase the number of prey patches.

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223   Another stealthiness index of predatory mites, the proportions of spider mite eggs laid on

224   webs in response to predator eggs, showed the same ranking, *i.e.*, the highest stealthiness in *P.*

225   *persimilis* and lowest in *N. womersleyi*. Because all of the predatory mites oviposited during the

226   experiments examining spider mite dispersal, the stealthiness index described above should in part

227   reflect the stealthiness of the deposited predatory mite eggs. Moreover, the ranking of the

228   stealthiness index was also consistent with both European and Japanese populations of *T. urticae*,

229   indicating that the stealthiness of predatory mites is not affected by the origin of the spider mite or

230   by the predatory mite populations tested. These results suggest that the relative levels of stealthiness

231   are consistent across prey mite species, although their absolute values may depend on the specific

232   combination of prey and predatory mite populations. Therefore, predator stealthiness could be used

233   as a novel index to evaluate the utility of predatory mite populations as biological control agents.

234   The stealthiness indices of the two commercialized biological control agents, *P. persimilis*

235   and *N. californicus*, were higher than those of *N. womersleyi*. This might not be coincidental if the

236   two predatory mites had been adopted as biological control agents based on their empirical utility in

237   crop fields, which should in part reflect their stealthiness to spider mites. In comparison, *N.*

238   *womersleyi* seems relatively unsuitable as a biological control agent against spider mites because the

239   predator failed to predate spider mites before dispersal, probably due to its low level of stealthiness

240   (but see Kondo, 2004 for a successful case in a greenhouse).

241   Considering the higher stealthiness of the other two species, *N. womersleyi* might have

242   potential for improved stealthiness. The low stealthiness (high detectability) of *N. womersleyi* eggs

243   seemed to be due to the existence of detectable surface materials rather than to the lack of special

244   concealing materials (Fig. 6b). Although *N. womersleyi* has much lower stealthiness than *P.*

245   *persimilis* and *N. womersleyi*, the mite thrives under natural conditions involving predation of spider

246   mites (McMurtry and Croft, 1997). Therefore, the inability of *N. womersleyi* to reduce such

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247 apparently maladaptive materials suggests that the materials have unknown adaptive functions,

248 which remain to be addressed in future investigations.

249 　　　The fitness of animals is largely affected by between-patch dispersal in environments where

250 opportunities to disperse are ensured (Bonte et al., 2012). Adult female spider mites disperse

251 between food patches primarily by walking (Brandenburg and Kennedy, 1982, Kennedy and Smitley,

252 1985, Margolies and Kennedy, 1985), although they disperse farther in response to predators

253 (Otsuki and Yano, 2014b). Dispersed spider mite females can establish local populations, which are

254 often in danger of extinction because of larger predatory insects (Janssen et al., 1998), coincidental

255 intra-guild predation by larger herbivores (Shirotsuka and Yano, 2012), and natural or

256 human-induced disturbance (*e.g.*, Das, 1959). Therefore, between-patch spider mite dispersal in

257 response to predatory mites with low stealthiness should in turn reduce the extinction rate of spider

258 mite metapopulations in the long term by increasing the number of local populations (Levins, 1969).

259 Although predator-induced prey dispersal seems maladaptive for predator individuals in the short

260 term, it may contribute to a stable prey supply for future offspring habitats. In other words,

261 predatory mites with low stealthiness may 'pasture' female prey mites, as long as prey eggs are

262 abundant within the intruded patch. Therefore, it is necessary to discuss whether high/low

263 stealthiness is advantageous to predatory mites in light of the metapopulation dynamics of both prey

264 and predatory mites.

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266 **Author Contribution Statement**

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275   **Conflict of interest**

276   The authors declare no conflict of interest.

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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

17

388 **Fig**. **3** The proportion of *T. kanzawai* females that dispersed (a) within and (b) between patches. C,

389 PP, NC, and NW indicate the control, *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments,

390 respectively. *$P < 0.05$, **$P < 0.001$ (Fisher's exact test with the Holm–Bonferroni correction).

391

392 **Fig**. **4** The proportion of *T. kanzawai* females preyed upon by each predatory mite species. PP, NC,

393 and NW indicate the *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. *$P <$

394 0.05, **$P < 0.01$, ***$P < 0.0001$ (Fisher's exact test with the Holm–Bonferroni correction).

395

396 **Fig**. **5** The proportions of *T. kanzawai* eggs laid on webs in response to eggs of each predatory mite

397 species. PP, NC, and NW indicate the *P. persimilis*, *N. californicus*, and *N. womersleyi* treatments,

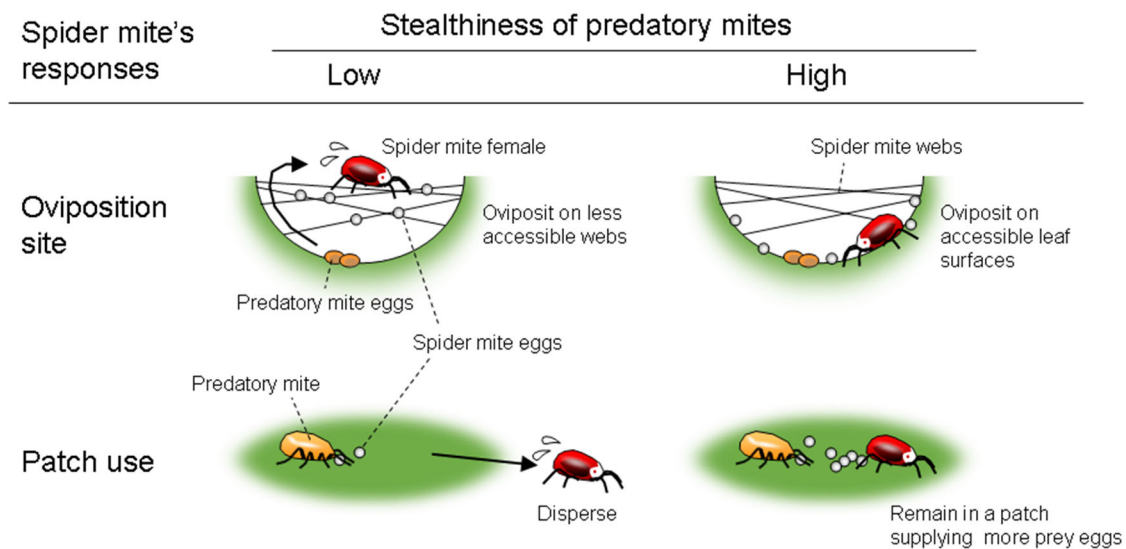398 respectively. *$P < 0.05$, ***$P < 0.0001$ (Steel–Dwass test).

399

400 **Fig**. **6** The proportions of *T. kanzawai* eggs laid on webs in response to untreated and washed

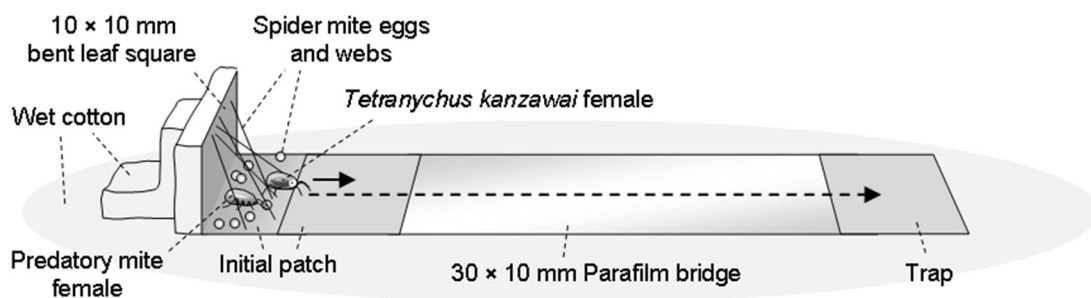401 predator eggs of (a) *P. persimilis* and (b) *N. womersleyi* (Mann–Whitney *U*-test).

402

403 **Fig**. **7** The proportions of eggs laid on webs by females of (a) European and (b) Japanese *T. urticae*

404 populations in response to eggs of the predatory mite species. PP, NC, and NW indicate the *P.*

405 *persimilis*, *N. californicus*, and *N. womersleyi* treatments, respectively. **$P < 0.001$, ***$P < 0.0001$
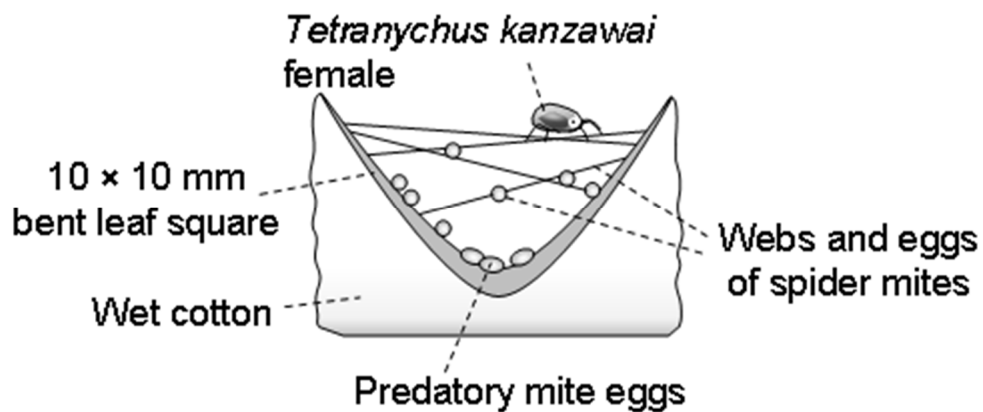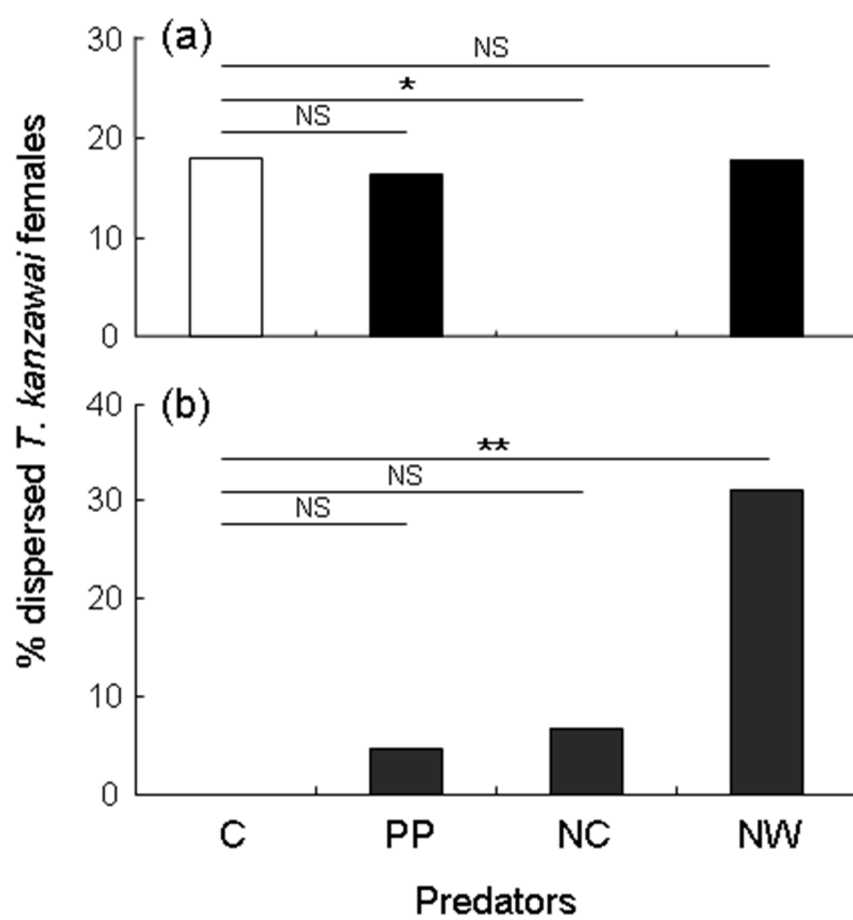
406 (Steel–Dwass test).

Graphical abstract

Spider mite's responses — Stealthiness of predatory mites (Low / High)

Oviposition site:
- Low: Spider mite female; Oviposit on less accessible webs; Predatory mite eggs; Spider mite eggs
- High: Spider mite webs; Oviposit on accessible leaf surfaces

Patch use:
- Predatory mite; Low: Disperse
- High: Remain in a patch supplying more prey eggs

Figure 1

10 × 10 mm bent leaf square; Spider mite eggs and webs; *Tetranychus kanzawai* female; Wet cotton; Predatory mite female; Initial patch; 30 × 10 mm Parafilm bridge; Trap

Figure 2

Tetranychus kanzawai female; 10 × 10 mm bent leaf square; Wet cotton; Webs and eggs of spider mites; Predatory mite eggs
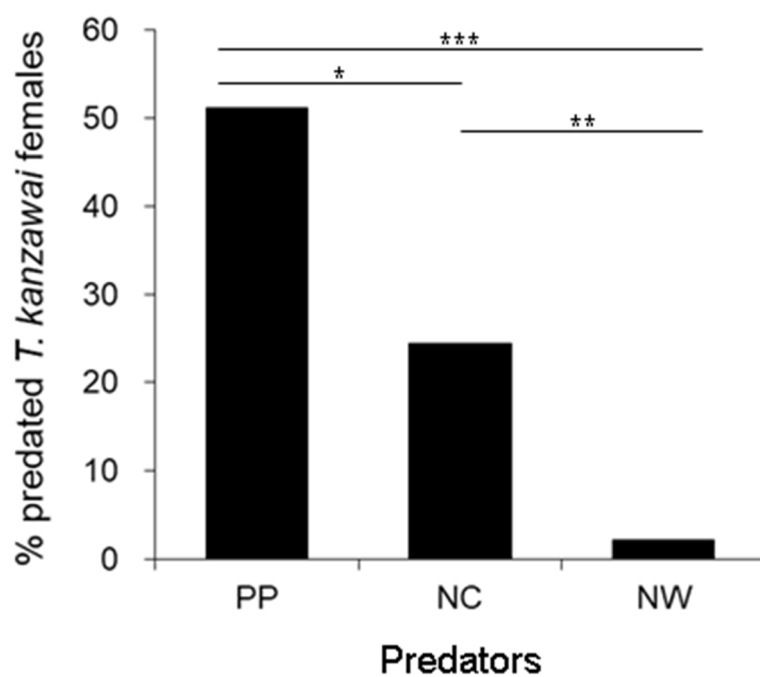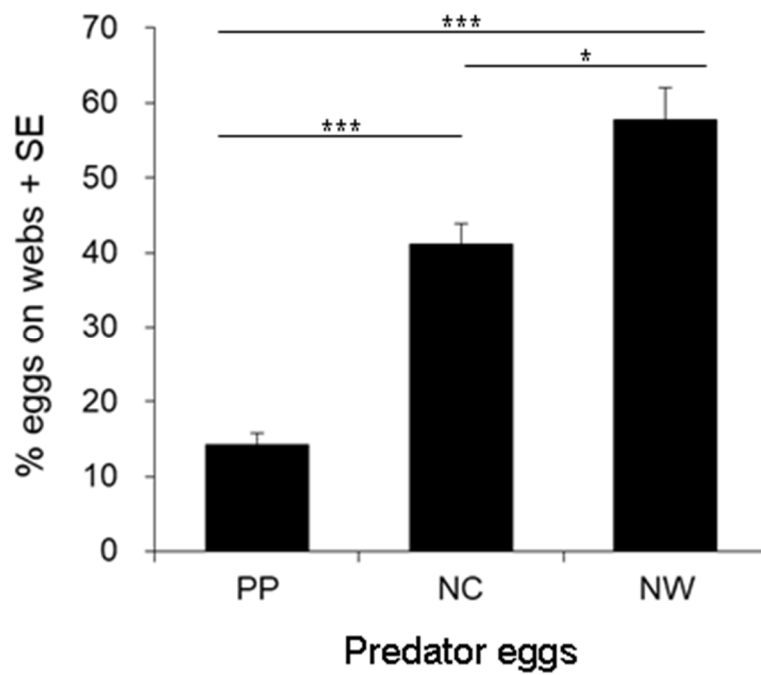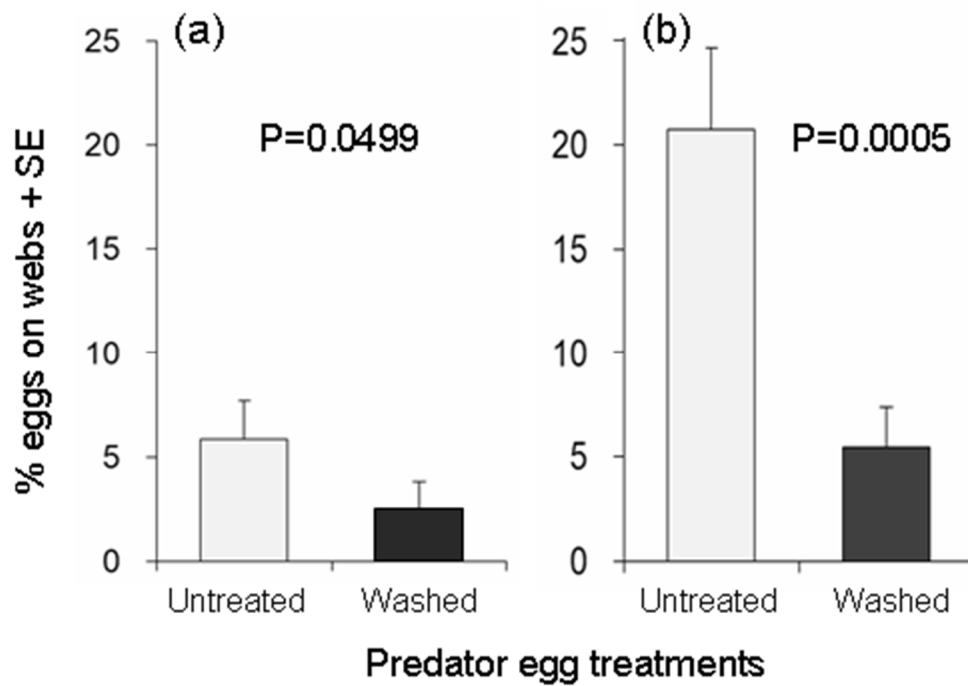
Figure 3

Figure 4

Figure 5

Figure 6

Figure 7