

1 **Cooperative web sharing against predators promotes group living in spider**

2 **mites**

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Abstract I examined spider mite cooperative web sharing against predation as a factor promoting group living. *Tetranychus urticae* and *Tetranychus kanzawai* infest leaf surfaces under webs made of silk threads. Experimental observation of predation by the predatory mite *Euseius sojaensis* on spider mites of different group sizes revealed that fewer spider mites were preyed upon when the web-building period before the attack was prolonged, suggesting that established webs help protect spider mites. Moreover, per capita predation on spider mites was diluted in larger groups. This was not due to predator satiation but seemingly because webs had been completed while the initial prey was consumed. Spider mites lived more closely together in the presence of a predator, showing that the degree of group living is facultative. In the presence of a preceding spider mite with an established web, a newcomer spider mite gain protection by taking residence in the established webs; sharing the web was not disadvantageous for the preceding mite. The proportion of individuals preyed upon did not differ between preceding and newcomer mites, suggesting that there was no interference against the latter. These interactions were consistent between heterospecific spider mites. Because there was no detectable

27 indirect interaction between mites sharing fresh webs, cooperative web sharing
28 seemed to be a major force promoting group living in the spider mites. Moreover, the
29 distances between spider mites did not differ between heterospecific and conspecific
30 groups, demonstrating that mites living together do not distinguish between species;
31 hence, heterospecific mites may cooperate and live together in the same manner as
32 conspecifics.

33

34 **Key words** Apparent interspecific cooperation ▪ dilution effect ▪ group size ▪ indirect
35 interaction ▪ cooperative web sharing

36 **Introduction**

37 Individuals living in a group can reduce their risk of predation by means of
38 cooperative defense, the dilution effect, and by early warning (Krause and Ruxton
39 2002 and references therein). On the other hand, group members incur costs in terms
40 of increased exposure to natural enemies and increased intraspecific competition
41 (Fitzgerald 1993; Rasa 1997; Prokopy and Roitberg 2001). Therefore, the degree of
42 conspecific aggregation should reflect the costs and benefits of group living (Rasa
43 1997; Spieler 2003; Semeniuk and Dill 2004; Despland and Huu 2007). From this
44 viewpoint, heterospecific individuals may also live together in a group when the
45 benefit of interspecific grouping to individuals overwhelms the cost of interspecific
46 competition between them. These interspecific interactions have been reported
47 among conspecific organisms such as birds (Krams and Krama 2002), spiders
48 (Hodge and Storfer-Issera 1997), shellfishes (Briones-Fourzan et al. 2008), and
49 mammals (Barry and Mundy 2002). This study reports that related spider mite
50 species with common potential predators live together and cooperate in the same
51 manner as conspecifics; this co-habitation is probably a byproduct of intraspecific

52 cooperation.

53 *Tetranychus urticae* and *Tetranychus kanzawai* are polyphagous spider mites
54 (e.g., Jeppson et al. 1975; Gotoh et al. 1999). They live together on dozens of wild
55 and cultivated host plant species and often co-occur on the same plant specimen
56 (Kondo and Takafuji 1985; Morishita 1992; 1997; Takafuji and Morishita 2001;
57 Osakabe et al. 2002; Ohno et al. 2010). Mated mite adult females (founder
58 individuals) construct complicated, irregular webs on leaf surfaces (Saito 1983),
59 feeding and reproducing inside the webs, and ultimately forming aggregations that
60 include juveniles that also contribute to the web building (Hazan, 1974; Clotuche et
61 al., 2009). Mated adult females of these mites disperse to new hosts, primarily by
62 walking (Kondo and Takafuji 1985; Margolies and Kennedy 1985; Morishita 1992;
63 1997). Ambulatory dispersing adult females of *T. urticae* often follow trails left by
64 preceding females and join webs built by conspecifics, which results in group living
65 at a new colony site (Yano 2008). Although mites normally aggregate on their host
66 plants (Strong et al. 1997; Oku et al. 2005; Yano 2008), a typical tetranychid colony
67 in the wild contains less than five adult females (Yano, unpublished data).

As an ultimate factor promoting conspecific group living of spider mites, cooperative defense against predators using webs has been reported in the bamboo spider mite *Stigmaeopsis longus* (Saito 1986a; 1986b; Mori et al. 1999). In contrast, virtually no attention has been paid to the benefit of group living as cooperative defense in either *T. urticae* and *T. kanzawai*. This may be because spider mites of this genus never exhibit aggressive defensive behaviors, though aggressive defense against predators does occur in mites belonging to the genus *Stigmaeopsis* and in social caterpillars (McClure and Despland 2011). Another reason for the lack of attention to the benefit of cooperative defense in *Tetranychus* may be that specialist predatory mites such as *Phytoseiulus persimilis* and *Neoseiulus womersleyi* can easily suppress spider mite populations at high densities (e.g., Chant 1961; Hamamura 1986), which implies that collective webs are ineffective as a defense. However, the apparently antagonistic interactions between spider mites and specialist predatory mites may only be one potential outcome because spider mite webs should exclude remaining potential predators. Indeed, some studies have suggested that spider mite webs are effective against generalist predators (McMurtry

et al. 1970; Sabelis and Bakker 1992). Therefore, interactions between spider mites and generalist predatory mites should be examined as a factor promoting spider mite group living.

In general, the effectiveness of a defensive trait against potential enemies becomes apparent only when the trait is absent. For example, some myrmecophytes are only heavily attacked by herbivorous insects when symbiont ants, i.e., the defensive trait of the plant, are artificially excluded from the plants (Vasconcelos 1991; Gaume et al. 1997). From this viewpoint, antagonistic interactions between spider mites and potential predators will be detectable only before founder spider mite females (that had dispersed from previous host plants) complete webs on new host plants. *Euseius sojaensis* is a generalist predatory mite that feeds on plant products and many spider mite species (Osakabe et al. 1986; Amano 1996). Although *E. sojaensis* cannot penetrate completed spider mite webs (Osakabe 1988; Ozawa and Yano 2009), the predatory mite readily preys on spider mites outside the webs (Ozawa and Yano 2009). Therefore, the predator is considered to be a typical potential predator of *T. urticae* and *T. kanzawai*.

In this study, I examine why the spider mite species *T. urticae* and *T. kanzawai* live in groups, and why different spider mite species may live close together, by investigating cooperative web sharing against the potential predator *E. sojaensis*.

Materials and methods

Mites

Single populations of the two spider mite species were collected in Kyoto, Japan; that of *T. urticae* (green form) was collected from a rose garden, and the *T. kanzawai* population was collected from a strawberry garden. Both populations were maintained on expanded primary leaves of the kidney bean *Phaseolus vulgaris* (Leguminosae), pressed onto water-saturated cotton in Petri dishes (90-mm diameter, 14-mm depth). The *E. sojaensis* study population was collected from kudzu vines *Pueraria lobata* (Willd) Ohwi (Leguminosae) in Kyoto and was reared on tea pollen on 50 × 50-mm squares of Parafilm (Parafilm M; American National Can Co.,

Chicago, IL, USA) placed on water-saturated cotton in Petri dishes (for details, see Shiotsuka and Yano 2011). The dishes were placed in transparent plastic containers and kept at $25 \pm 2^{\circ}\text{C}$ and $50 \pm 5\%$ relative humidity, with a photoperiod of 16L8D (hereafter described as “laboratory conditions”).

Adult females of the spider and predatory mites used in the following experiments were similar in size (≤ 0.5 mm). Detailed observations and transfer using a fine brush were possible only under a stereomicroscope. Webs are usually invisible even under a microscope (e.g., Clotuche et al. 2009). Because mated adult females represent the dispersing stage of spider mites, I used 2- to 4-day-old mated females (hereafter “females”) of *T. urticae* and *T. kanzawai* in the following experiments. By using these females as prey, I simulated an early stage of web building in the presence or absence of predators.

Effects of group size and webs on predation rates on spider mites

To examine effects of spider mite group size and the degree of web building on

132 predation by *E. sojaensis*, I confined different numbers (1, 2, and 4) of each spider
133 mite species on 15 × 15-mm bean leaf squares. Unless otherwise noted, I thereafter
134 used bean leaf squares of the same size. One to four adult females correspond to a
135 typical colony size of tetranychid mites in the wild (Yano, unpublished data). I then
136 introduced an *E. sojaensis* female onto each leaf square after different time lags (0, 1,
137 4, and 24 h), which allowed spider mites to build different degrees of webs before
138 predator attack. I did not monitor at more frequent intervals because spider mites
139 seem to have diurnal rhythms (e.g., Clotuche et al. 2011). I used 3- to 5-day-old
140 starved *E. sojaensis* females that had previously been isolated for 48 h in 1.5-ml
141 microtubes (Treff AG, Degersheim, Switzerland) with a water droplet. This was to
142 promote immediate predation and to easily judge predation, because the transparent
143 body of a starved predator turns a vivid vermillion after consuming prey. Thereafter,
144 all starved *E. sojaensis* were prepared in the same manner. No *E. sojaensis* females
145 died during the starvation treatment. The number of replicates for each combination
146 of group sizes and time lags was >20. Preliminary experiments showed that
147 predation by a starved *E. sojaensis* female on a *T. urticae* or a *T. kanzawai* female on

a leaf square reached a plateau 12 h after introduction (Fig. 1). Therefore, the proportion of consumed prey (predation rates) in all experiments was measured 24 h after predator introduction. The data were analyzed with a Wald test (SAS Institute Inc. 1998).

To examine whether satiation of the predators may have limited predation rates of the above experiment, potential consumption by *E. sojaensis* was measured. To prepare living prey females that do not walk or produce webs, I used adult females of *T. urticae* and *T. kanzawai* that had been subjected to a sub-lethal intensity of ultraviolet irradiation (253.7-nm wavelength, 0.45 W m⁻² for 1 h) using a GL-6 sterilization lamp (6 W; Ultra-Violet Box, Sogorikagaku Glass Works Co., Kyoto, Japan). I supplied four prey females to each starved predatory mite on a leaf square. After 24 h, the number of consumed prey was recorded.

To examine whether spider mite eggs deposited during the experimental period may have affected predation rates in the experiment, egg consumption by *E. sojaensis* in the same period was examined. I confined a female of each spider mite species on the bean leaf squares. After 24 h, I carefully removed the females with

164 minimal damage to the webs, and counted the number of eggs laid. All spider mite
165 eggs were deposited within webs. I then introduced a starved *E. sojaensis* onto each
166 leaf square. After another 24 h, I counted the number of consumed eggs.

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168 Degree of spider mite group living in response to a predator

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170 To examine whether spider mites lived together in response to predators, I measured
171 the distance between pairs of spider mite females in relation to predator presence. I
172 introduced two females onto each of 24 leaf squares for each spider mite species. To
173 avoid predation during observation, I allowed the females to build webs for 24 h
174 under laboratory conditions, after which the females were sufficiently protected by
175 webs (see “Results”). I then introduced one starved *E. sojaensis* female each onto
176 half of the leaf squares ($n = 12$, predator presence) for each spider mite species while
177 the rest of the squares served as controls ($n = 12$, predator absence for each species).
178 Because the body length of *E. sojaensis* was <0.5 mm, leaf area occupied by the
179 predator was $<1/1,000$ of the leaf square, which may be considered negligible. After

1, 4, and 24 h, I measured the distances between the centers of the idiosomas of the female spider mites to the nearest 1 mm as a degree of group living. As decimal fractions were rounded off, the minimum distance was 1 mm. A replicate (*T. urticae*, predator absence) in which a spider mite female escaped from the leaf square was excluded from the data. A three-way ANOVA (SAS Institute Inc. 1998) was then performed on square root-transformed data.

Pros and cons of lodging and hosting spider mites in the presence of a predator

To simulate the conditions in which a preceding spider mite female has already established a web, an initial female (hosting female) was introduced to a leaf square. After 24 h, when the whole surface of the leaf square was more or less covered by web, a second lodging female and a starved *E. sojaensis* female were introduced to the square. To discriminate between conspecific spider mites, I randomly selected one and marked it with a dab of blue pigment ink on the dorsal setae. I examined four combinations (i.e., *TuTu*, *TkTk*, *TuTk* and *TkTu*) of the two spider mite species.

The number of replicates for each combination was >20. Predation rates were measured 24 h after predator introduction.

To examine costs and benefits of hosting and lodging, predation rates on hosting and lodging females were compared with those in the absence of respective partners. Thus, the predation rate on lodging females was compared with that of solitary females without webs (group size = 1, time lag = 0 h in the above experiment) while that on hosting females was compared with that on solitary females with webs (group size = 1, time lag = 24 h). The rates were compared using Fisher's exact probability test.

Indirect interaction between spider mites sharing webs in the absence of a predator

Indirect interactions among herbivores include both exploitative competition and plant-mediated interactions (e.g., Kaplan and Denno 2007). To examine whether there were either competitive or facilitative indirect interactions between spider mite females sharing webs, I introduced one female (initial female) onto each of forty 10

212 × 10-mm leaf squares per species (*T. urticae* and *T. kanzawai*); 40 squares served as
213 controls without initial females. These leaf squares were maintained under
214 laboratory conditions. After 24 h, I carefully removed the initial females with
215 minimal damage to the webs, and counted the number of eggs laid. I then introduced
216 one *T. urticae* female (test female) each onto half of the leaf squares in each
217 treatment and one *T. kanzawai* female (test female) onto each of the remaining
218 squares. After another 24 h, I counted the cumulative egg numbers laid and
219 calculated egg numbers laid by each test female by subtracting the egg number of the
220 initial female from the cumulative number. Because the number of eggs laid within a
221 certain period is considered the most sensitive performance index of spider mite
222 females (Yano et al. 1998; Gotoh et al. 1999; Agrawal 2000; Yano et al. 2003), any
223 indirect interaction, either exploitative competition or plant mediated interaction,
224 between females sharing webs should result in lower (or higher) egg numbers laid by
225 the test female. A one-way ANOVA (SAS Institute Inc. 1998) was performed on the
226 data for each test female species.

227

228 Do spider mites living together distinguish between species?

229

230 To examine whether females living together distinguish between species, I
231 introduced two females onto a 15 × 15-mm leaf square in the following
232 combinations: two *T. urticae* (n = 32), two *T. kanzawai* (n = 31), or one female of
233 each species (n = 33). I then measured the distances between females to the nearest 1
234 mm at 3, 6, 12, 24, and 48 h after the introduction. A one-way ANOVA (SAS
235 Institute Inc. 1998) was performed on square root-transformed data for each time
236 point.

237

238 **Results**

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240 Effects of group size and webs on predation rates on spider mites

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242 Both group size and time lag for web building had significant effects on per
243 capita predation rates on *T. urticae* and *T. kanzawai* (Table 1). Decreased predation

with increased time lag indicates that completed webs may effectively defend spider mites from predation while decreased (per capita) predation with increasing group size indicates a dilution effect (Fig. 2). Each *E. sojaensis* individual consumed less than one spider mite in average.

The number ($\pm$ SE) of immobilized spider mites consumed by *E. sojaensis* individuals in 24 h was 2.24 ± 0.17 ($n = 21$) for *T. urticae* and 3.30 ± 0.16 ($n = 20$) for *T. Kanzawai*. These results demonstrate that predators consuming at most one living spider mite in a 24-h period in this experiment were not satiated. Predators may have consumed less active spider mites rather than those that were immobilized because of the protection provided by webs and the mobility of prey mites (possible avoidance behavior).

In addition, the number ($\pm$ SE) of spider mite eggs consumed by *E. sojaensis* individuals in 24 h was 0.43 ± 0.23 ($n = 14$) for *T. urticae* and 1.08 ± 0.46 ($n = 13$) for *T. Kanzawai*, while initial egg numbers were 7.21 ± 0.49 ($n=14$) and 9.00 ± 0.60 ($n=13$), respectively.

Degree of spider mite group living in response to a predator

The distances between females differed significantly with respect to the presence of a predator (Table 2), although the differences became less obvious over time after predator introduction (Fig. 3). Thus, spider mite females lived more closely together in response to predator presence. In addition, no spider mites were preyed upon during this experiment.

Pros and cons of lodging and hosting spider mites in the presence of a predator

The predation rates on lodging and hosting females did not differ significantly (Table 3, comparison A), suggesting that there was no interference against lodging females. Indeed, interference behaviors among females were never observed. Moreover, the predation rate on lodging females was lower than that on solitary mites without webs (Table 3, comparison B); the predation rate on hosting females did not differ from that on solitary females with webs (Table 3, comparison C). These patterns were

276 consistent across all combinations of spider mite species.

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278 Indirect interaction between spider mites sharing webs in the absence of a predator

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280 The number of eggs laid by a test female within 24 h did not differ among treatments

281 for either *T. urticae* (Fig. 4a), *T. kanzawai* (Fig. 4b), indicating that there was

282 virtually no indirect interaction between heterospecific and conspecific mites sharing

283 fresh webs.

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285 Do spider mites living together distinguish between species?

286

287 Up to 24 h after introduction, the average distance between spider mite females was

288 approximately 3 mm (on a 15 × 15-mm square) for all combinations. That is, the

289 mites lived relatively close together even in the absence of a predator. The distance

290 between females did not differ significantly among heterospecific and conspecific

291 groups at any point; $P = 0.18$ (3 h), 0.84 (6 h), 0.42 (12 h), 0.49 (24 h), and 0.25 (48

h) (Fig. 5). These data show that spider mite females living together do not distinguish between species.

Discussion

The decrease in predation on spider mites with increased time lag for web building indicates that established webs protected spider mites from predation. Previous studies (McMurtry et al. 1970; Osakabe 1988; Sabelis and Bakker 1992; Ozawa and Yano 2009) also report that established spider mite webs are effective against generalist predators. Although spider mite webs contain many eggs, all eggs are deposited within webs where *E. sojaensis* cannot easily access. Therefore, *E. sojaensis* consumed only a small fraction of the eggs. Moreover, considering the relative size of a spider mite (0.5 mm) and an egg (<0.15mm; Crooker 1985), effects of egg consumption on predation rates seemed negligible, if any. Compared with the spider mite short generation time of about 10 days at 25°C, a web establishment period as long as 24 h may be considerable. Therefore, any trait that reduces

predation risk during this 24-h period should confer selective advantage to the spider mites. From this viewpoint, group living during web production seems to reduce the predation rate on spider mites. This dilution effect was not due to the satiation of predatory mites because they had the potential to consume more than twice the number of immobilized prey in the same period. Therefore, it is likely that the tested predatory mites were unable to consume more living prey because webs had been completed beforehand.

The closer group living of spider mites in the presence of a predator implies that the degrees of group living in the two spider mite species are facultative; i.e., the benefit of closer group living in the presence of a predator may outweigh its possible cost. Because no spider mite was preyed upon in the presence of previously established webs, indirect cues for predator presence, e.g., odors from injured conspecifics (Grostal and Dicke 1999; Oku et al. 2003), may be ruled out; the spider mites living closely together may have instead detected direct cues for predator presence, e.g., odors and wastes (Grostal and Dicke 1999, 2000; Pallini et al. 1999). The closer group living of spider mites in the presence of a predator had decreased

over time probably because amount of established webs may have affected spider mites' behaviors and/or because they became increasingly aware that predators were unable to access them.

Dispersing adult females of *T. urticae* readily follow conspecific trails and join conspecific webs (Yano 2008). The benefit of these behaviors was explicitly demonstrated in the present study in the practice of cooperative web sharing. In the presence of a predator and a preceding spider mite with an established web, a secondarily introduced (lodging) female gained protection from predation by lodging in the web: sharing the web was not a disadvantage for the hosting female. This asymmetric cost-benefit of lodging and hosting females seems to explain why they shared webs. Otherwise, if the benefit of a lodging individual were achieved at a cost for the hosting individual, such altruistic behavior should have evolved only between conspecific relatives. Moreover, the proportion of predated individuals did not differ between hosting and lodging mites, suggesting that there was no interference against the latter. The above interactions were consistent in pairs of heterospecifics, indicating that spider mites sharing webs do not distinguish between species.

Although there was no direct interference between spider mites sharing webs, living in proximity to others may have fitness costs associated with indirect competition, i.e., exploitive and/or plant-mediated competition (Tilman 1982; Kaplan and Denno 2007). However, such indirect competition seemed negligible both within and between spider mite species sharing webs. Because the feeding modes of the two related spider mite species were identical, fine-scale resource partitioning between individuals living in close proximity (e.g., Daugherty 2009) seems unlikely. Oku et al. (2009) demonstrated a web-building cost for *T. urticae* adult females in terms of reduced egg production during the initial 24 h of web building. Therefore, females introduced secondarily may have offset the costs of possible indirect competition with initial females by reducing web-building costs, that is, by sharing established webs. There may be some competition after web establishment, i.e., following the initial 24 h of web building; however, living in proximity to others after the initial 24 h would no longer be necessary because spider mites were seldom preyed upon after that time. The rarity of predation after this 24 h period is attributable to (1) spider mites remaining within webs and (2) continued

feeding within webs that are extended over leaf surfaces, leading to heavy infestation (Yano, unpublished data). Web extension in this manner is reflected in Figure 5, which shows that between-female distances increased slightly after 24 h of web building. Therefore, living in proximity to others during web establishment should always be advantageous in the end, perhaps explaining why the spider mites always live in groups. Le Goff et al. (2010) reported significant positive group effects on egg production in *T. urticae* virgin females. However, such a positive group effect on egg production was not detected in the present experiment using mated females (i.e., dispersing stage) of the two spider mite species.

Although the two spider mite species co-occur on the same host plants (Kondo and Takafuji 1985; Morishita 1992; 1997; Takafuji and Morishita 2001; Osakabe et al. 2002; Ohno et al. 2010) and have the potential to live closely together on a single leaf, as demonstrated here, strong natural selection for heterospecific cooperation (in comparison to conspecific cooperation) remains questionable. The apparent cooperation between heterospecifics may rather be a byproduct of cooperation between conspecifics that live together. The two spider mite species discriminate to

some extent between heterospecific and conspecific mates before copulation (Ozawa and Takafuji 1987), suggesting that there has been selection for discrimination between species when necessary. Therefore, the fact that the spider mites did not distinguish between species when living together on a leaf likely indicates that some advantage is gained by sharing webs with heterospecifics.

There is a complete post-mating reproductive barrier between *T. urticae* and *T. kanzawai* (Ozawa and Takafuji 1987), indicating that they are distinct biological species. Therefore, the apparent cooperative web sharing between these two species raises the question of how the two distinct species evolved. The most plausible explanation may be allopatric speciation; *T. urticae* expanded its distribution to southwestern areas of Japan (Kyoto) as recently as the late 1970s (Gotoh and Shinkaji 1981).

Although spider mite webs afford effective protection against generalist predatory mites, the webs are ineffective against mites that specialize in preying on web-spinning spider mites (McMurtry et al. 1970; Sabelis and Bakker 1992). This is an example of apparent trade-offs in adaptation to different prey (Levins and

MacArthur 1969). Moreover, some specialist predatory mites use spider mite webs as prey-searching cues (Pratt and Croft 1999; Roda et al. 2001; Furuichi et al. 2005). Therefore, group living of spider mites may be costly against such specialist predatory mites. This possible trade-off in cooperative web sharing against specialist and generalist predatory mites may in turn determine spider mite optimal group sizes in the wild; this is a topic that remains to be addressed in future investigations.

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570

Figure Legends

Fig. 1 A preliminary test confirming predation saturation over time. There was no predation of spider mite females after the initial 12 h. Hence, predation rate was measured subsequently 24 h after predator introduction.

Fig. 2 Effects of group size and webs on predation rates on spider mites. *Bars* indicate per capita predation rate on active (a) *T. urticae* and (b) *T. kanzawai* with different group sizes and time lags for web building. Decreased predation with increased time lag indicates that completed webs may effectively defend spider mites from predation while decreased (per capita) predation with increasing group size indicates a dilution effect.

Fig. 3 Degree of spider mite group living in response to a predator. Distances between conspecific spider mites are shown in relation to predator presence 1, 4, and 24 h after predator introduction. Spider mites lived more closely together in response to predator presence, although the differences became less obvious over time after

587 predator introduction.

588

589 **Fig. 4** Indirect interactions between spider mites sharing a web in the absence of a
590 predator. The number of eggs laid by a test female within 24 h did not differ among
591 treatments for either a *T. urticae* and b *T. kanzawai*, indicating that there was
592 virtually no indirect interaction between heterospecific and conspecific mites sharing
593 fresh webs.

594

595 **Fig. 5** Do spider mites living together distinguish between species? *Lines* indicate
596 distances between spider mite females. There were no significant differences among
597 the three groups at any point, suggesting that spider mite females living together do
598 not distinguish between species.

Fig.1

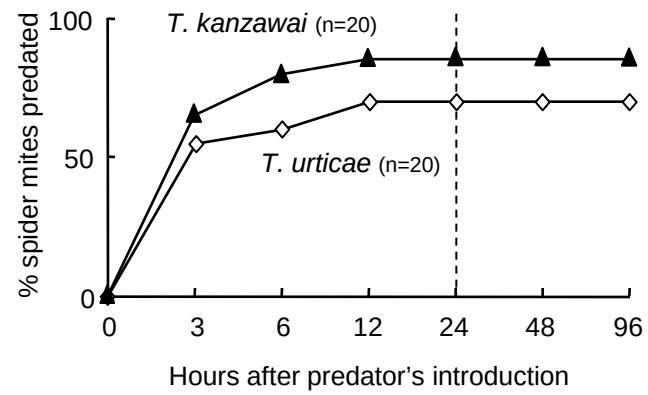


Fig.2

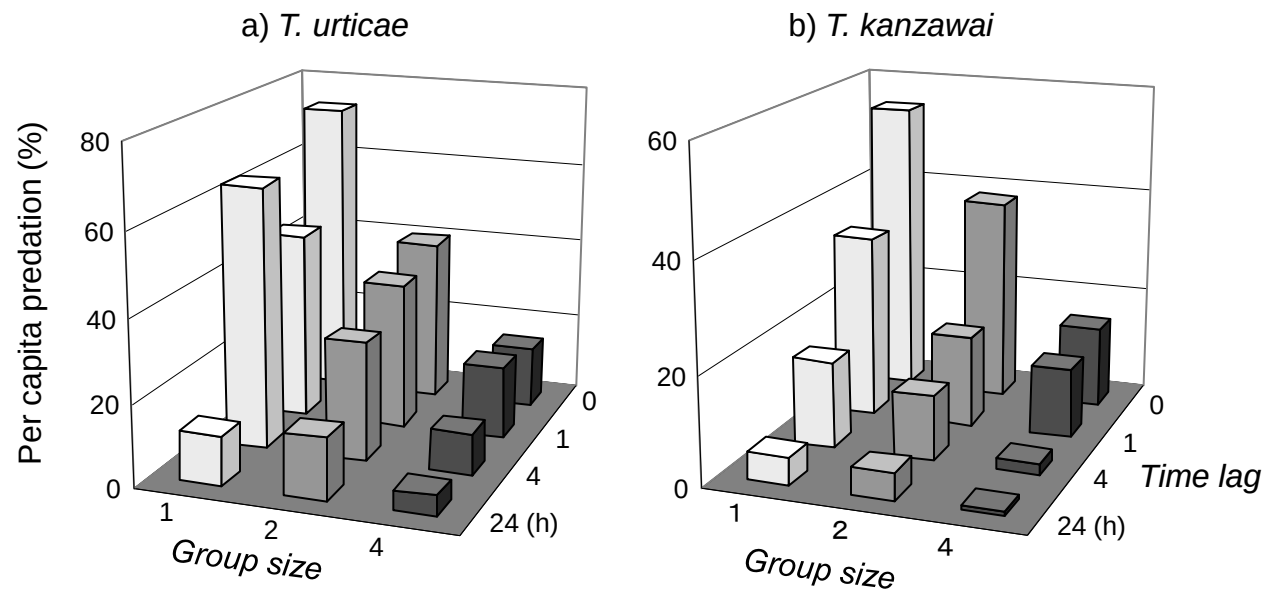


Fig.3

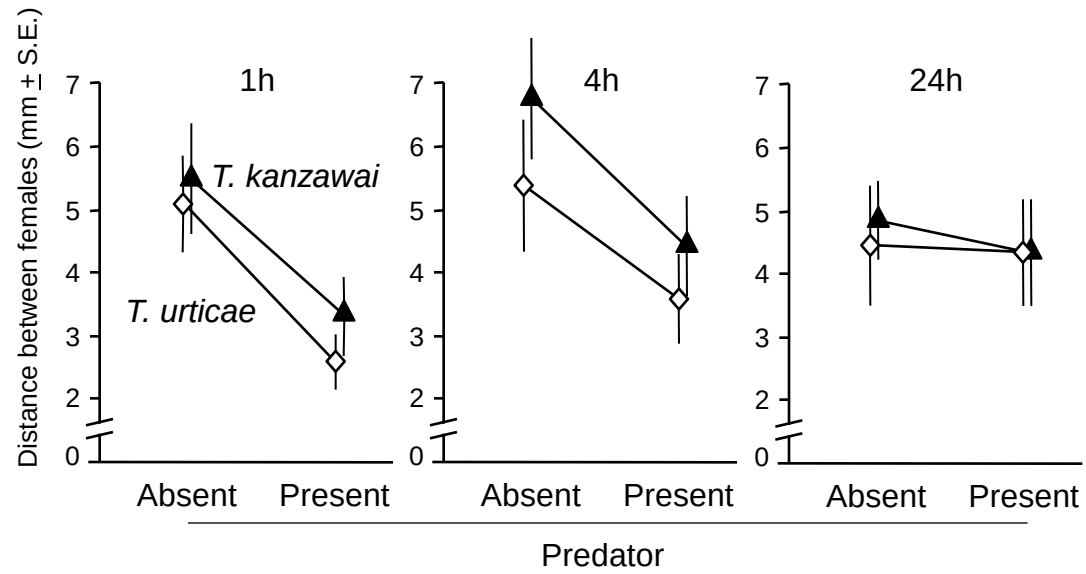


Fig.4

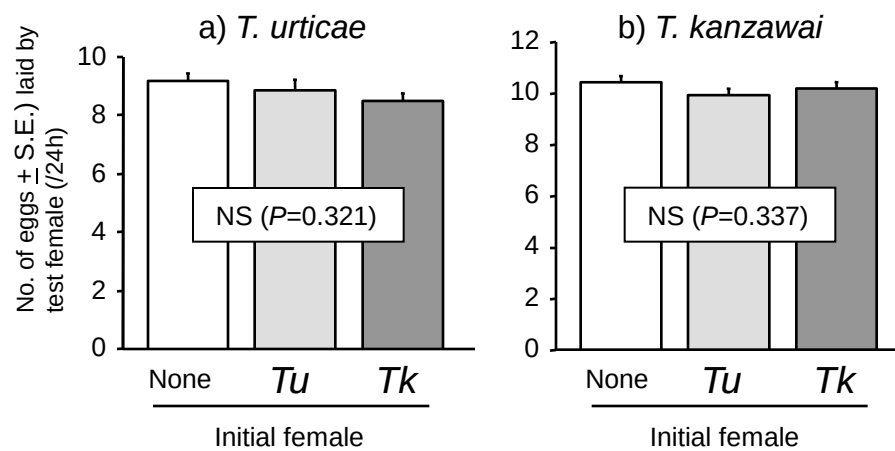


Fig.5

