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# Oviposition-site shift in phytophagous mites reflects a trade-off between predator avoidance and rainstorm resistance

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1 **Oviposition-site shift in phytophagous mites reflects a trade-off between predator**

2 **avoidance and rainstorm resistance**

3

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9 **Abstract**

10 Predators can reduce prey population densities by driving them to undertake costly  
11 defences. Here, we report on a remarkable example of induced antipredator defence in  
12 spider mites that enhances the risk to rainstorms. Spider mites live on the undersides of  
13 host plant leaves and usually oviposit on the leaf undersurface. When they are  
14 threatened by predatory mites, they oviposit on three-dimensional webs to avoid egg  
15 predation, although the cost of ovipositing on webs has not yet been clearly determined.  
16 We prepared bean plants harbouring spider mite (*Tetranychus kanzawai*) eggs on either  
17 leaf surfaces or webs and exposed them to rainstorms outdoors. We found that fewer  
18 eggs remained on webs than on leaf surfaces. We then examined the synergistic effect  
19 of wind and rain by simulating both in the laboratory. We conclude that ovipositing on  
20 webs comes at a cost, as eggs are washed off the host plants by wind and rain. This may  
21 explain why spider mite populations decrease drastically in the rainy season, although  
22 they inhabit leaf undersides where they are not directly exposed to rainfall.

23

24 **Keywords:** non-consumptive effect ▪ oviposition site shift ▪ *Tetranychus kanzawai* ▪  
25 wind and rain ▪ synergistic effect

26

27 **1. Introduction**

28           Anti-predator defences generally incur fitness costs that are outweighed by the  
29 benefit of predator avoidance [1]. Costs associated with defence induction result from  
30 reduced foraging [2–4] and enhanced risk of predation by other species [5–7] or  
31 exposure to abiotic stressors [8]. The induction of costly defences can be seen as a  
32 non-consumptive effect of predators that control prey population density [9, 10].

33           Spider mites in the genus *Tetranychus* are commonly found on the undersides  
34 of host plant leaves [11, 12]. They construct three-dimensional protective webs that are  
35 not waterproof, but are effective at deterring generalist predators [13]. The females  
36 usually lay their eggs on the leaf surface under the webs, where the offspring feed and  
37 grow. However, predatory mites that specialise on spider mites will invade the webs  
38 [14] and feed preferentially on spider mite eggs [15, 16]. In response to these attacks,  
39 adult female spider mites disperse from the invaded patches [4, 17, 18] or oviposit on  
40 the webs instead [19–22], an action we refer to as an oviposition site shift. These eggs  
41 are attached to complicated and irregular silk threads [23]. Far fewer eggs on webs are  
42 eaten compared with those on leaf surfaces before predators leave the prey patches [22].  
43 Predator-experienced spider mite females oviposit on webs even in the absence of  
44 predators [21, 22]. Because spider mite females typically do not oviposit on webs when  
45 the predation risk is low, and predator-induced oviposition site shift declines with time  
46 in the absence of such risks [21, 22], the fitness costs associated with this induced  
47 defence may be considerable. Nonetheless, the costs have not yet been clearly detected.  
48 Although fewer spider mite eggs are observed in the presence of predators [4], this  
49 reduction may reflect the costs of both the oviposition site shift and avoidance activities  
50 such as dispersal attempts from predator-intruded patches [22]. However, the cost of an

51 oviposition site shift has not been detected in terms of reduced egg numbers or reduced  
52 survival of adult females in the absence of predators, suggesting that the cost of an  
53 oviposition site shift is negligible in terms of the above fitness indices [22]. Moreover,  
54 ovipositing females and eggs on webs are not exposed to enhanced predation risks by  
55 other predators that cannot access spider mite webs [7, 13].

56 Empirical observations have shown that spider mite populations decline  
57 drastically in the rainy season in summer [24, 25]. Therefore, rainfall may have a  
58 negative effect on spider mites. However, the control of spider mite populations by  
59 rainfall seems inconsistent with the fact that spider mites usually live on leaf undersides  
60 [11, 26], where they are not directly exposed to rainfall [12].

61 This study examined the effects of stormy weather, which may wash mite eggs  
62 on webs away. First, the persistence of spider mite eggs on webs and leaf surfaces on  
63 host plants after exposure to stormy weather outdoors was compared. Then, the  
64 synergistic effect of wind and rain was examined by simulating both factors in the  
65 laboratory. Based on the results, the vulnerability of mite eggs on webs to rainstorms  
66 will be discussed as a major non-consumptive effect of predators that may control  
67 spider mite populations in the wild.

68

## 69 **2. Materials and methods**

### 70 (a) Mites

71 The *T. kanzawai* study population was collected from trifoliolate orange trees (*Poncirus*  
72 *trifoliata*) in 2018 in Kyoto, Japan. Mites were reared on the expanded primary leaves  
73 of kidney bean plants (*Phaseolus vulgaris* L.), which were pressed onto water-saturated  
74 cotton in Petri dishes (“leaf disks”). The population was maintained on predator-free

75 leaf disks for more than 10 generations. *Neoseiulus womersleyi* is a native predator of *T.*  
76 *kanzawai* in Japan [27]. The *N. womersleyi* individuals were collected from bushkiller  
77 plants (*Cayratia japonica* [Thunb.] Gagnep.) in 2015 in Kyoto and reared on leaf disks  
78 infested heavily with *Tetranychus urticae* Koch as prey for ca. 100 generations. The leaf  
79 disks were placed in transparent containers maintained at 25°C and 50% relative  
80 humidity under a 16L:8D photoperiod.

81

82 (b) Eggs on webs vs. leaf surfaces in stormy weather

83 Kidney bean plants with one expanded primary leaf left on the stem were cut at the  
84 same height (10 cm) and individually inserted into 10-mL glass tubes filled with water.  
85 The tubes were fixed on the bottoms of plastic trays at intervals of > 8 cm to prevent  
86 leaves from touching each other. To induce spider mite oviposition on webs, we  
87 prepared *T. kanzawai* females at 2–4 days post maturation that had previously been  
88 exposed to *N. womersleyi* using the method of Murase et al. [21]. These  
89 predator-experienced females oviposit mainly on webs, even in the absence of predators,  
90 whereas predator-naïve females of the same age oviposit mainly on leaf surfaces [21,  
91 22]. Females were introduced individually to the undersides of the bean leaves. After 24  
92 h, females and eggs in a contradictory position (i.e., eggs of predator-experienced  
93 females on leaf undersurfaces and eggs of predator-naïve females on webs) were  
94 carefully removed using fine insect pins so that all eggs on each leaf were laid either on  
95 webs or leaf surfaces. This procedure was necessary because eggs initially on webs are  
96 often retained on leaf surfaces after exposure to rain (S. Okada and S. Yano  
97 unpublished). The number of eggs on each plant was recorded, and the plants were  
98 exposed to rain on July 27 (3 h, ca. 20 mm) and July 31 (1 h, > 30 mm, accompanied by

99 strong winds; a typical seasonal shower) in 2019. Plants used on July 27 and 31 were  
100 different ones. We used 11 replicate plants harbouring eggs on webs and 12 on leaf  
101 surfaces on July 27, and nine replicates on webs and 12 on leaf surfaces on July 31.  
102 After exposure to rain, the plants were transferred indoors on the same day and the  
103 numbers of eggs that had remained on the leaves were counted after the leaves had dried.  
104 The proportions of remaining eggs were compared using the Mann-Whitney U test  
105 (SAS 9.22; SAS Institute Inc., Cary, NC; nonparametric test) due to extreme  
106 non-normality and overdispersion of the data, which occurred because all or no eggs  
107 tended to remain on each plant, depending on whether the webs harbouring eggs were  
108 washed away or not.

109 To confirm that *T. kanzawai* oviposits on webs in the wild, we examined *C.*  
110 *japonica* leaves infested by *T. kanzawai* on the campus of Kyoto University on  
111 September 5 (n = 21) and September 20 (n = 30), 2019. We counted the numbers of  
112 eggs on both webs and leaf surfaces at the site under a stereomicroscope.

113

#### 114 (c) The synergistic effect of wind and rain

115 To experimentally examine the synergistic effect of wind and rain on spider mite eggs  
116 on webs, both wind and rain were simulated in the laboratory. Bean plants harbouring  
117 mite eggs on either webs or leaf surfaces were prepared in the manner described above.  
118 The bean plants were assigned one of four treatments: (a) both wind and rain, (b) rain  
119 only, (c) wind only, and (d) neither wind nor rain. All bean plants were arranged in 3 × 2  
120 matrices in plastic trays in the manner described above. To adjust the number of plants  
121 receiving wind and/or rain, dummy bean plants without eggs were placed on trays  
122 containing fewer than six test plants. For the wind treatment, unheated wind (ca. 14 m/s)

123 was alternately applied from both of the tray's longer sides using a hair dryer  
124 (KHD-9000; Koizumi Seiki, Osaka, Japan) in a laboratory sink. The dryer was held 10  
125 cm from the nearest bean plant and was moved so as to apply equal amounts of wind to  
126 every plant (Fig. 2c). This process lasted for approximately 20 s in total, which equalled  
127 the time required for the subsequent rain treatment. There were 16 replicates with eggs  
128 laid on webs and 12 on leaf surfaces. For the rain treatment, 1500 mL of water (25°C)  
129 was sprayed equally onto the 20 × 30 cm area of the tray, which corresponded to 25 mm  
130 of rainfall. The water was sprayed from 10 cm above the nearest bean plant through a  
131 PET bottle lid with nine 3-mm-diameter holes. The size of artificial raindrop was ca.  
132 5mm in diameter. The bottle was squeezed and moved so as to spray an equal amount of  
133 water on every plant (Fig. 2b). There were 12 replicates with eggs laid on webs and 11  
134 on leaf surfaces. For the wind and rain treatment, the bottle lid was moved closer to the  
135 position of the hair dryer so that slanting water droplets would hit the plants directly  
136 (Fig. 2a). This manipulation also lasted for 20 s in total. There were 16 replicates with  
137 eggs on webs and 14 on leaf surfaces. The plastic trays of the control treatment (neither  
138 wind nor rain) were placed in the sink for 20 s. There were 13 replicates with eggs on  
139 webs and 17 on leaf surfaces. The numbers of eggs remaining after each treatment were  
140 counted after the leaves had dried. Although the experiment was conducted with a  
141 factorial design, proportions of remaining eggs were compared among all treatments  
142 and oviposition sites using a nonparametric multiple comparison (Steel-Dwass all pairs,  
143 SAS 9.22) due to extreme non-normality and overdispersion of the data.

144

### 145 3. Results

146 (a) Eggs on webs vs. leaf surfaces in stormy weather



147 The proportions of remaining eggs did not differ between oviposition sites on July 27  
148 with rainfall ( $p = 0.131$ , Mann-Whitney U test; Fig. 1a). However, on July 31, with a  
149 sudden downpour accompanied by strong winds, more than 80% of the eggs on webs  
150 were lost, and significantly fewer eggs remained on webs compared to leaf surfaces ( $p =$   
151  $0.0002$ , Mann-Whitney U test; Fig. 1b).

152 The mean  $\pm$  standard error proportions of *T. kanzawai* eggs on webs on wild *C.*  
153 *japonica* leaves were  $19.35\% \pm 7.37\%$  ( $n = 21$ ; Sep 5) and  $34.30\% \pm 7.02\%$  ( $n = 30$ ;  
154 Sep 20), indicating that the mites do oviposit on webs in the wild.

155

156 (b) The synergistic effect of wind and rain

157 The proportions of eggs remaining on webs under both wind and rain was significantly  
158 lower than the rest of all groups ( $p < 0.01$ , Steel-Dwass all pairs; Fig. 2). Although wind  
159 or rain alone tended to wash some eggs away on webs, their effects were not significant  
160 (Fig. 2). That is, wind and rain seemed to have a synergistic effect on eggs on webs.

161

#### 162 4. Discussion

163 The cost of a predator-induced shift in oviposition site in spider mites has been  
164 demonstrated. That is, more mite eggs on webs were washed away from host plants  
165 compared to those on leaf surfaces during a typical rainstorm. Because spider mite eggs  
166 exhibit water tolerance [28] and *T. kanzawai* is a polyphagous herbivore [12], some  
167 larvae that hatch from eggs that are located on alternative host plants may have a chance  
168 to survive. Otherwise, larvae that are ca. 0.1 mm in length will face difficulty in  
169 returning to their original host plants due to limited mobility. This cost may prevent  
170 spider mites from ovipositing on webs under low predation risk. Although local

171 rainstorm frequency data were unavailable, the maintenance of predator-induced  
172 oviposition site shifting in spider mites suggests that the benefit of this behaviour is  
173 greater than its cost on average.

174         The different results obtained in the two outdoor experiments in rainy weather  
175 suggest that a factor other than rain is responsible for washing away mite eggs on webs.  
176 To examine this possibility, wind and rain were simulated in the laboratory, and a  
177 synergistic effect of the two factors was suggested. It is likely that only raindrops  
178 carried by strong wind can hit mite eggs on webs on leaf undersides, whereas raindrops  
179 alone cannot. By contrast, most eggs on leaf surfaces remained on the plant despite both  
180 wind and rain. That is, mite eggs are safe during strong rainstorms as long as they are  
181 deposited on leaf surfaces, suggesting that spider mites oviposit on hazardous webs  
182 largely to avoid predators. The results potentially explain the long-standing mystery of  
183 why wild spider mite populations decline drastically in the rainy season [24, 25],  
184 although mites usually live on leaf undersides [11, 26] where they are sheltered from  
185 direct rainfall [12].

186         The washing away of mite eggs on webs can be seen as a remarkable example of  
187 non-consumptive control of herbivores by predators. The non-consumptive effects of  
188 predators on prey are sometimes comparable to those of direct consumption [10, 29–31].  
189 This also seems true in the spider mite system and is explained as follows. An adult  
190 female *N. womersleyi* consumes ca. 12 *T. kanzawai* eggs per day at 25°C [32]. Every  
191 predator-experienced *T. kanzawai* female oviposited on webs, even in the absence of  
192 predators for more than 6 days [22]. The peak oviposition rate of a *T. kanzawai* female  
193 is >10 eggs per day [33], and the development time of the eggs is ca. 5 days at 25°C  
194 [34]. Therefore, a *N. womersleyi* female can potentially cause a shift in the position of

195 dozens or hundreds of *T. kanzawai* eggs onto webs for several days, and every  
196 rainstorm during the period would wash away >80% of these eggs (see Results).

197 In spider mites, some non-consumptive effects of predators have been reported.  
198 Predatory mite intrusion into spider mite webs decreases the foraging time of spider  
199 mites seeking refuge on webs and results in fewer eggs [4]. Moreover, spider mites that  
200 moved off their webs in response to predatory mite intrusion are more likely to be  
201 preyed upon by other predators that do not intrude into the webs [7]. In addition to these  
202 non-consumptive effects, a predator-induced shift in oviposition site onto webs that  
203 sometimes results in most of the eggs being washed away should be seen as a major  
204 non-consumptive effect of predators controlling spider mite populations.

205

206 **Data accessibility.** All data can be found in the electronic supplementary material.

207 **Authors' contributions.** S.Y. conceived the study. S.O. and S.Y. conducted experiments.

208 S.O. and S. Y. wrote the manuscript. Both authors approved the final version of the  
209 manuscript and agree to be held accountable for the content therein.

210 **Competing interests.** We declare we have no competing interests.

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317

318 **Captions**

319 Figure 1. Persistence of eggs on webs and leaf undersurfaces after exposure to wind and  
320 rain. Horizontal bars represent mean values. Plot sizes represent initial egg numbers.

321 Figure 2. The synergistic effect of wind and rain on spider mite eggs. Horizontal bars  
322 represent mean values. Different letters indicate significant difference at  $p < 0.01$   
323 (Steel-Dwass all pairs).

324

Figure 1

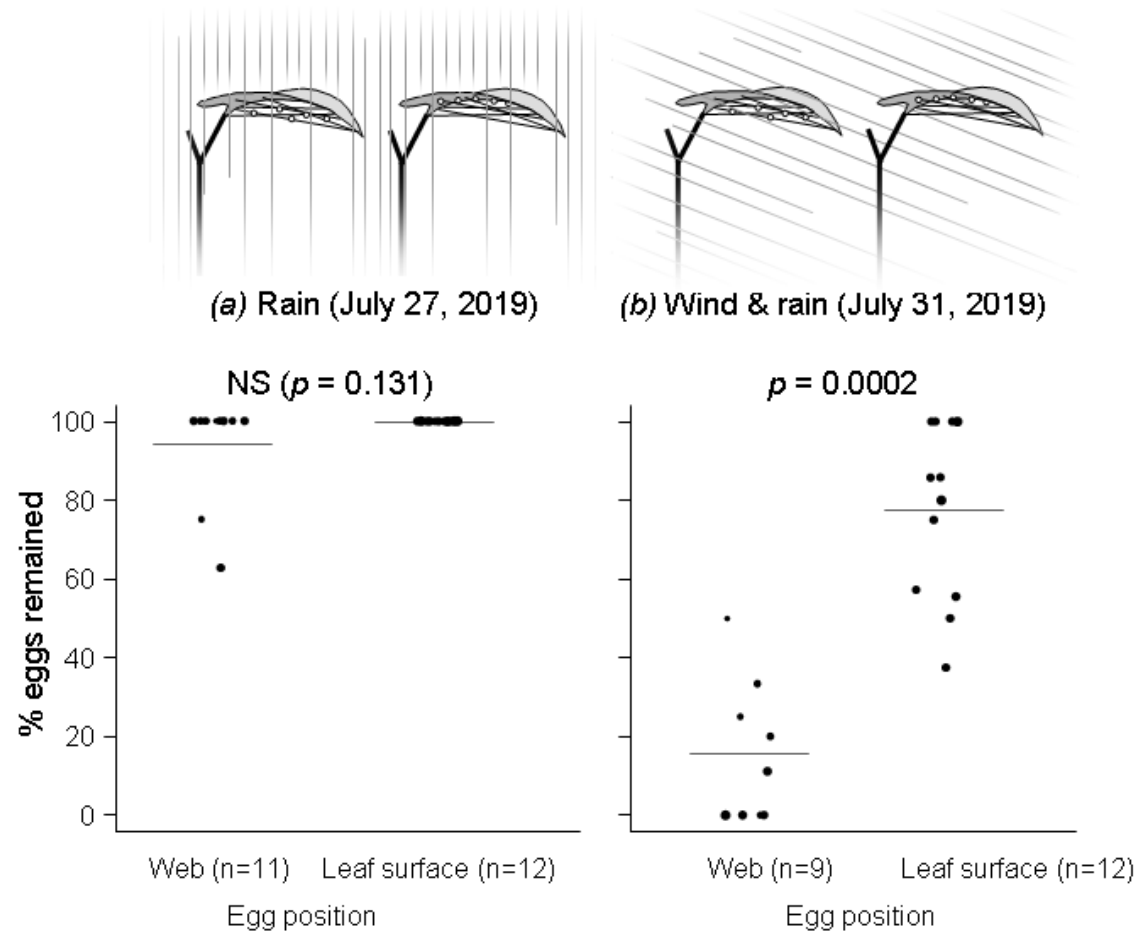




Figure 2

