

Coincidental intraguild predation by caterpillars on spider mites

Shirotsuka Kanako and Yano Shuichi

Laboratory of Ecological Information Department of Agriculture Kyoto University Sakyo-ku, Kyoto, 606-8502, Japan

Laboratory of Ecological Information

Graduate School of Agriculture Kyoto University Sakyo-ku, Kyoto, 606-8502, Japan

Laboratory of Ecological Information

+81-75-753-6135

+81-75-753-6135

kshiro@kais.kyoto-u.ac.jp

Abstract

Intraguild predation (IGP) is defined as the killing and eating of prey species by a predator that also can utilize the resources of the prey. It is mainly reported among carnivores that share common herbivorous prey. However, a large chewing herbivore could prey upon sedentary and/or micro herbivores in addition to utilizing a host plant. To investigate such coincidental IGP, we observed the behavioral responses of the polyphagous mite *Tetranychus kanzawai* Kishida (Acari: Tetranychidae) when its host plant *Cayratia japonica* (Thunb.) Gagnep. (Vitaceae) was attacked by hornworms, *Theretra japonica* Boisduval (Sphingidae) and *T. oldenlandiae* Fabricius (Sphingidae). We also examined an interaction between the oligophagous mite *Panonychus citri* McGregor (Acari: Tetranychidae) and caterpillars of the swallowtail *Papilio xuthus* L. (Papilionidae) that share citrus plants as their main food source. Although all *T. kanzawai* and some active stage *P. citri* tried to escape from the coincidental IGP, some were consumed together with eggs, quiescent mites, and host plant leaves, suggesting that coincidental IGP occurs on spider mites in the wild. Moreover, neither hornworms nor swallowtail caterpillars distinguished between spider mite-infested and uninfested leaves, suggesting that the mite-infested leaves do not discourage caterpillar feeding. The reasons that the mites have no effective defense against coincidental IGP other than escaping are discussed.

Keywords: coincidental intraguild predation; herbivorous; hornworm; swallowtail; Tetranychus kanzawai; Panonychus citri

Introduction

Intraguild predation (IGP), the killing and eating of prey species by a predator that also can utilize the resources of the prey (Polis et al. 1989), is reported among predators that share common herbivorous prey, as well as among omnivores and herbivores that share common plant resources (e.g., Pallini et al. 1998; Montserrat 2008). Growing evidence indicates the importance of IGP among predators in many natural communities (Holt and Polis 1997; Roda et al. 2001; Kaneko 2007). As numerous herbivore species with a variety of feeding modes coexist on the same plant species (Strong et al. 1984), a large chewing herbivore may accidentally prey upon resident and/or micro-herbivores together with host plant tissues. Polis et al. (1989) defined this type of intraguild predation as ‘coincidental IGP.’ Langellotto et al. (2006) reported coincidental IGP among parasitoids in which ectoparasitoids consume host insects that have been previously parasitized by endoparasitoids. Although coincidental IGP seems to be widespread (Janzen, 1977; Polis et al., 1989), no study has ever examined coincidental IGP on spider mites by large herbivores that exclusively feed on plants.

As some predators have developed effective defenses against IGP (e.g., Faraji et al. 2000; Roda et al. 2001), prey species among herbivores may also have behavioral or other means of adaptation to avoid coincidental IGP by chewing herbivores when the herbivores impose serious selection pressure on the prey.

The polyphagous spider mite *Tetranychus kanzawai* Kishida (Acari: Tetranychidae) feeds on *Cayratia japonica* (Thumb.) Gagnep (Vitaceae) (Oku and Yano 2007; Ozawa et al. 2009). The plant is also infested by the hornworms *Theretra japonica* Boisduval (Sphingidae) and *Theretra oldenlandiae* Fabricius (Sphingidae) (Mutuura et al. 1965). The final instar hornworm consumes more than 20 *C. japonica* leaves (8 cm in length, 4 cm in width) in 24 h, and often exhausts individual *C. japonica* plants (Shiotsuka, personal observation). Therefore, the hornworms may accidentally prey upon spider mites together with *C. japonica* leaves. Moreover, a hornworm exhausts one *T. kanzawai* colony on

C. japonica within a few minutes whereas native predatory mites such as *Neoseiulus womersleyi* Schicha (Acari: Phytoseiidae) can take several days to accomplish this. Therefore, hornworms may impose selection pressure on *T. kanzawai* in the same way as predatory mites, and hence the mite may also have some countermeasure to avoid coincidental IGP by the hornworms. We also observed the interactions between the citrus red mite *Panonychus citri* McGregor (Acari: Tetranychidae) and the swallowtail butterfly, *Papilio xuthus* L. (Papilionidae), which share citrus plants as their main food. Compared to *T. kanzawai*, *P. citri* should frequently encounter herbivorous guild members; hence, the interactions over coincidental IGP on the plants should be more conspicuous.

Thus, by examining the IGP on both polyphagous and oligophagous spider mites by caterpillars, we intended to examine the generality of coincidental IGP and possible countermeasure against it in this system.

Materials and Methods

Plants

Cayratia japonica is a perennial vine commonly found around agricultural fields and shrubs from the tropical to the temperate zones in Asia (Makino 1982) that is often infested by the herbivorous mite *Tetranychus kanzawai* (Oku and Yano 2007; Ozawa and Yano. 2009). The leaves are pedately compound with each leaf consisting of five leaflets (Satake et al. 1982). All *C. japonica* leaves used in the following experiments were obtained from the campus of Kyoto University.

Poncirus trifoliata L. (Raf.) is a deciduous citrus shrub. The leaves are compound with each leaf consisting of three leaflets (Satake et al. 1989). This species is often used for hedging in Japan.

Caterpillars

The hornworms, *Theretra japonica* and *T. oldenlandiae* feed on Vitaceae plants from June to October in Japan (Mutuura et al. 1965). We collected the eggs and larvae of both hornworms from *C. japonica* and reared them on *C. japonica* leaves. The first to fourth instars were individually reared in 200-ml transparent

cups with air holes, while the fifth instars were individually reared in 900-ml cups. The cups were maintained at 25°C, 50% relative humidity, and L16/D18 photoperiod (hereafter laboratory conditions).

Papilio xuthus feeds on citrus plants from March to October in Japan (Fukuda et al. 1982). We collected eggs and larvae of *P. xuthus* from *P. trifoliata* and reared them on *P. trifoliata* leaves under laboratory conditions. The first to fourth instars were individually reared in 200 ml plastic transparent cups, and the fifth instars were reared in 900 ml cups.

Mites

Tetranychus kanzawai is a polyphagous mite that infests various wild and cultivated plants (e.g. Gomi and Gotoh 1996). We used two *T. kanzawai* populations (wild and laboratory populations) collected from *C. japonica* in Kyoto, Japan. The wild strain was collected as needed in 2010 and temporarily maintained on *C. japonica* leaves under laboratory conditions prior to the following experiments. The laboratory strain had been maintained on expanded leaves of the kidney bean *Phaseolus vulgaris* L. and pressed onto water-saturated cotton in Petri dishes (90 mm diameter, 14 mm depth; hereafter bean leaf discs) under laboratory conditions since 2000.

Panonychus citri is a serious citrus pest of citrus plants (e.g., Shinkaji 1979). The study population of *P. citri* was collected from *P. trifoliata* and maintained on bean leaf discs in the manner described above.

The approximate body length of an adult female mite is <0.5 mm, while that of fifth instar caterpillars is 80 mm (hornworms) and 40 mm (*P. xuthus*).

Coincidental IGP on polyphagous mites: Kanzawa spider mites preyed upon by hornworms

Behavioral avoidance of T. kanzawai against hornworm feeding

To observe the behavioral responses of *T. kanzawai* when attacked by hornworms, we collected *C. japonica* leaves infested by *T. kanzawai* (wild strain) and inserted them individually into a 2-ml tube bottle filled with water until the subsequent experiment. We also introduced three mated *T. kanzawai* females

(laboratory strain) onto each uninfested *C. japonica* leaf prepared in the same manner and maintained them under laboratory conditions. After 10 days, *T. kanzawai* individuals of all developmental stages were present on each leaf. We then presented the infested *C. japonica* leaves to a fifth instar hornworm (*T. japonica* and *T. oldenlandiae*). We continuously observed caterpillars using stereomicroscopes and scored every contact with all mite stages. Therefore, the number of available observations (see Results) differed among the developmental stages (egg, larva, nymph, adult, quiescent) of the mites. Because observations were made only when caterpillars had vigorously consumed leaves, possible differences in preference among caterpillar individuals were not reflected in the data. Therefore, each encounter was treated as independent data. The data for the active stages (larva, nymph, adult) were subjected to a Wald test (SAS Institute Inc. 1998) to determine the effects of developmental stage and mite strain.

Preference of hornworms for T. kanzawai-infested leaflets

To determine whether hornworms avoided feeding on *T. kanzawai*-infested leaves, we conducted dual choice tests. This test was performed to examine whether spider mite-infested leaves may somehow discourage caterpillar feeding. We removed all leaflets except for a single pair of detached *C. japonica* compound leaves, which were inserted into a 2-ml tube bottle filled with water (Fig. 1-a). We then introduced three mated adult female *T. kanzawai* onto one of the leaflets, banded the petiole with wet cotton to prevent the mites from escaping, and maintained the setup under laboratory conditions. After 24 h, when all mites had settled on the introduced leaflet, we removed the cotton and introduced a fifth instar hornworm to the bottom edge of the leaf to observe which leaflet the caterpillar targeted first (Fig. 1-b). This experiment was repeated 24 times using 11 *T. japonica* caterpillars and 30 times using 29 *T. oldenlandiae* caterpillars. New leaves and new spider mites were used for every replicate. The data were subjected to a Wilcoxon signed-ranks test to control for possible differences in preference among individual caterpillars.

As the only choice for a wingless caterpillar seems to be whether to feed on or to leave an encountered plant, we examined whether the caterpillars refused to feed on *T. kanzawai*-infested leaves. We introduced a fifth-instar *T. oldenlandiae* caterpillar onto a detached *C. japonica* compound leaf infested by three *T.*

kanzawai females. This test was conducted only for *T. oldenlandiae* (18 replications using six caterpillars). We then observed whether the caterpillars fed on or left the leaves.

Coincidental IGP on oligophagous mites: citrus red mites preyed upon by swallowtail caterpillars

Behavioral avoidance of P. citri against P. xuthus feeding

To observe the behavioral responses of *P. citri* when attacked by *P. xuthus* caterpillars, we collected *P. trifoliata* leaves infested by *P. citri*. These leaves were presented to a fifth-instar *P. xuthus* and we observed coincidental IGP on *P. citri* individuals in the same manner described above. The data for the active stages were subjected to a chi-square test.

Preference of P. xuthus caterpillars for P. citri-infested leaflets

To determine whether *P. xuthus* caterpillars avoided feeding on *P. citri*-infested leaves, we removed the center leaflet of a detached *P. trifoliata* compound leaf and confined two mated female *P. citri* onto one of the leaflets in the manner described above (Fig. 2-a). After 24 h, we introduced a fifth instar *P. xuthus* caterpillar (19 replicates using five caterpillars) and observed which leaflet the caterpillars targeted first (Fig. 2-b). The data were subjected to a Wilcoxon signed-ranks test.

To examine whether the caterpillars refused to feed on *P. citri*-infested leaves, a fifth-instar *P. xuthus* caterpillar was introduced onto a detached *P. trifoliata* compound leaf infested by two *P. citri* females (19 replications using five caterpillars). We then observed whether the caterpillars fed on or left the leaves.

Results

Coincidental IGP on polyphagous mites: Kanzawa spider mites preyed upon by hornworms

*Behavioral avoidance of *T. kanzawai* against hornworm feeding*

All eggs and quiescent mites were consumed together with *C. japonica* leaves by hornworms (Fig. 3). The proportions of consumed mites did not differ between mite strains, but did among the developmental stages of the mite (Table. 1). Although nearly all mites in the active stages tried to escape attack, mature mites were less likely to be consumed (Fig. 3). Some female adult mites escaped from infested leaves via petioles or by traveling over the body surface of the hornworms.

*Preference of hornworms for *T. kanzawai*-infested leaflets*

Neither hornworm species distinguished leaflets infested by *T. kanzawai* from uninfested ones (Fig. 4a, b). No tested hornworms (out of 29 trials for *T. oldenlandiae* and 24 trials for *T. japonica*) refused to feed on the provided leaves, and all leaves were eventually fully consumed. Moreover, when provided only with infested leaves, no tested *T. oldenlandiae* caterpillars (out of 18 trials) refused to feed on the leaves, suggesting that the caterpillar does not refuse spider mite-infested leaves as a rule.

Coincidental IGP on oligophagous mites: citrus red mites preyed upon by swallowtail caterpillars

*Behavioral avoidance of *P. citri* against *P. xuthus* feeding*

All eggs and quiescent mites were consumed together by a *P. xuthus* caterpillar with *P. trifoliata* leaves (Fig. 5). The proportions of consumed active mites differed significantly among mite stages, indicating that mature mites are less likely to be consumed ($\chi^2 = 18.72$, $P < 0.001$; Fig. 5).

Preference of P. xuthus for P. citri-infested leaflets

Papilio xuthus caterpillars did not distinguish between leaflets infested by *P. citri* and uninfested ones (Fig. 4c). No tested *P. xuthus* caterpillars (out of 19 trials) refused to feed on provided leaves, and all leaves were eventually consumed. Moreover, when provided only with infested leaves, only one tested *P. xuthus* caterpillars (out of 23 trials) refused to feed on the leaves, suggesting that the caterpillar does not refuse spider mite-infested leaves as a rule.

Discussion

All tested caterpillar species consumed the spider mites together with the host plant leaves. Since the degree of spider mite infestation on the leaves was similar to that in the wild (Shirotsuka, personal observation), any coincidental IGP observed between herbivores could also be expected under natural conditions. There are some examples of IGP on spider mites by omnivores that feed on both herbivores and their host plants (Trichilo and Leigh, 1986; Pallini et al., 1997; Agrawal and Klein, 2000; Magalhães et al., 2005). According to the terminology proposed by Polis et al. (1989), this is the first report of coincidental IGP on spider mites by herbivores that exclusively feed on plants. We predict that such coincidental IGP should be universal between giant grazers and spider mites given that we observed two examples from the two interactions examined. Such overlooked interactions could explain, at least in part, the unknown mortality of spiders and other small herbivores in the wild.

All of the *T. kanzawai* individuals as well as some *P. citri* in active stages tried to escape coincidental IGP. Although ambulate migration of some spider mites is triggered by predator-associated odors (Magalhães et al., 2002), ambulate escaping of *T. kanzawai* and *P. citri* may have been triggered by physical stimuli rather than odor-based stimuli because the mites only showed escaping behavior after being attacked by the caterpillars. Even when *T. kanzawai* can successfully escape from caterpillar attack, it will incur a fitness cost of losing all relatives in the quiescent stages along with their shelter (webs). Therefore, any trait of *T. kanzawai* that helps it to avoid hornworm attack would be favored. However, neither hornworm species avoided feeding on *T. kanzawai*-infested leaves, suggesting that the mite-infested leaves do not discourage caterpillar feeding. Despite serious damage to *T. kanzawai* populations on *C. japonica* caused by

hornworms, it may be an evolutionarily rare event for the mite, which feeds on hundreds of host plant species (e.g., Gomi and Gotoh 1996). Otherwise, as some plant species systemically induce chemical defenses in response to spider mite infestation (Karban and Carey, 1984), the mites may have systemically altered the quality of both infested and uninfested leaflets.

Given the results of these experiments, we hypothesized that an oligophagous mite *P. citri* that shares citrus host plants with swallowtails in time and space would have developed effective avoidance mechanisms against the intraguild predator. However, more *P. citri* individuals appeared to be consumed by caterpillars compared to *T. kanzawai*, although the proportions of consumed mites cannot be directly compared given the differences among intraguild predator species. Unexpectedly, several active stage *P. citri* individuals did not move, even when under attack by the caterpillar. This characteristic appears maladaptive unless it has overwhelming benefits under other conditions, such as against predators other than swallowtail caterpillars. This remains to be examined in future studies.

Like *T. kanzawai*, *P. citri* exhibited no adaptations for avoiding coincidental IGP by swallowtail caterpillars other than escaping. Since spider mites have developed a variety of predator avoidance tactics against predatory mites (Grostal and Dicke 1999; Pallini et al. 1999, 2000; Oku et al. 2003), coincidental IGP by randomly feeding giant caterpillars is likely less important compared to predation by the predatory mites that directly search for the prey spider mites (e.g., Hoy and Smilanick 1981; Sabelis and Van de Baan 1983). In addition, since the caterpillars always consume plant leaves irrespective of spider mite infestation, the caterpillars would not benefit the shared prey (plants), unlike the case of IGP among predators, which seems to often benefit shared prey (herbivores), depending on the conditions (Janssen et al. 2007).

Acknowledgements

We thank two anonymous reviewers for helpful comments. We also thank members of the Laboratory of Ecological Information for valuable suggestions and encouragement. This work was supported by the Japan Society for the Promotion of Science [Basis Research C; grant number 21580066 to S. Y.].

References

- Agrawal, A. A. and Klein, C. N. (2000) What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores. *J. Anim. Ecol.* 69: 525-535
- Faraji F., Janssen A., Van Rijn P. C. J. and Sabelis M. W. (2000) Kin recognition by the predatory mite *Iphiseius degenerans*: discrimination among own, conspecific, and heterospecific eggs. *Ecol. Entomol.* 25: 147-155.
- Fukuda, H., Hama, E., Kuzuya, T., Takahashi, A., Takahashi, M., Tanaka, B., Wakabayashi, M. and Watanabe, Y. (1982) The life histories of butterflies in Japan. Vol. 1. Hoikusha Publishing Co., Ltd., Osaka. pp. 101-105
- Gomi, K. and Gotoh, T. (1996) Host plant preference and genetic compatibility of the Kanzawa spider mite, *Tetranychus kanzawai* Kishida (Acari: Tetranychidae). *Appl. Entomol. Zool.* 31: 417-425
- Grostal P. and Dicke M. (1999) Direct and indirect cues of predator risk influence behavior and reproduction of prey: a case for acarine interactions. *Behav. Ecol.* 10: 422-427
- Holt R. D. and Polis G. A. (1997) A theoretical framework for intraguild predation. *Am. Nat.* 149: 745-764
- Hoy, M. A. and Smilanick J. M. (1981) Non-random prey location by the phytoseiid predator *Metaseiulus occidentalis*: differential responses to several spider mite species. *Entomol. Exp. Appl.* 29: 241-253
- Janssen, A., Sabellis, M. W., Magalhães S., Montserrat, M. and Van der Hammen, T. (2007) Habitat structure affects intraguild predation. *Ecology* 88: 2713-2719
- Janzen, D. (1977) Why fruits rot, seeds mold, and meat spoils. *Am. Nat.* 111:691-713
- Kaneko, S. (2007) Predator and parasitoid attacking ant-attended aphids: effects of predator presence and attending ant species on emerging parasitoid numbers. *Ecol Res* 22:451-458
- Karban, R. and Carey J. R. (1984) Induced resistance of cotton seedlings to mites. *Science* 225:53-54
- Langellotto, G. A., Rosenheim, J. A. And Williams, M. R. (2006) Assessing trophic interactions in a guild of primary parasitoids and facultative hyperparasitoids: stable isotope analysis. *Oecologia.* 150: 291-299
- Magalhães S., Janssen A, Hanna R. and Sabelis M. W. (2002) Flexible antipredator behaviour in herbivorous mites through vertical migration in a plant. *Oecologia.* 132: 143-149
- Magalhães, S., Janssen, A., Montserrat, M. and Sabelis, M. W. (2005) Host-plant species modifies the diet of an omnivore feeding on three trophic levels. *Oikos* 111: 47-56
- Makino T. (1982) Rhamnales Vitaceae. In: Honda, M. (ed.) Makino's illustrate of flora in colour. Hokuryukan Co., Ltd., Tokyo. pp.322
- Montserrat M., Magalhães S., Sabelis M. W., De Roos A. M. and Janssen A. (2008) Patterns of exclusion in an intraguild predator-prey system depend on initial conditions. *J Anim. Ecol.* 77: 624-630

- Mutuura, A., Yamamoto, Y. and Hattori, I. (1965) Sphingidae. In: Early stages of Japanese moths in colour vol. 1. (Revised by Isshiki, S.) Hoikusha Publishing Co., Ltd., Osaka. pp.26-28
- Oku, K. and Yano, S. (2007) Spider mites (Acari: Tetranychidae) deform their host plant leaves: an investigation from the view point of predator avoidance. *Entomol. Soc. Am.* 100: 69-72
- Oku, K., Yano, S. and Takafuji, A. (2003) The use of a refuge during the quiescent stage spider mites in the presence of a predator. *Entomol. Exp. Appl.* 108: 71-74
- Ozawa, M. and Yano, S. (2009) Pearl bodies of *Cayratia japonica* (Thumb.) Gagnep. (Vitaceae) as alternative food for a predatory mite *Euseius sojaensis* (Ehara) (Acari: Phytoseiidae). *Ecol Res* 24:257-262
- Pallini, A., Janssen, A. and Sabelis, M. W. (1997) Odour-mediated responses of phytophagous mites to conspecific and heterospecific competitors. *Oecologia* 110: 179-185
- Pallini A., Janssen A. and Sabelis M. W. (1998) Predators induce interspecific herbivore competition for food in refuse space. *Ecol. Lett.* 1:171-177
- Pallini A., Janssen A. and Sabelis M. W. (1999) Spider mites avoid plants with predators. *Exp. Appl. Acarol.* 23:803-815
- Polis G. A., Myers C. A. and Holt R. D. (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297-330
- Roda A., Nyrop J., EEnglish-Loeb G. and Dicke, M. (2001) Leaf pubescence and two-spotted spider mite webbing influence phytoseiid behavior and population density. *Oecologia* 129: 551-560
- Sabelis M. W. and Van de Baan H. E. (1983) Location of distant spider mite colonies by Phytoseiid predators: demonstration of specific kairomones emitted by *Tetranychus urticae* and *Panonychus ulmi*. *Entomol. Exp. Appl.* 33:303-314
- SAS Institute Inc. (1998) SAS/STAT user's guide, release 6.03 edition. SAS Institute, Cary.
- Satake, Y., Ohwi, J. Kitamura, S., Watari, S. and Tominari, T. (1982) Wild flowers of Japan. Herbaceous plants (including Dwarf Subshrubs). Heibonsha Ltd., Tokyo. p.238
- Satake, Y., Hara, H., Watari, S. and Tominari, T. (1989) Wild flowers of Japan. Woody plants. Heibonsha Ltd., Tokyo. p.282
- Shinkaji, N. (1979) Geographical distribution of the citrus red mite, *Panonychus citri* and European red mite, *P. ulmi* in Japan. In; Recent Advances in Acarology, vol. 1 (J. G. Rodriguez, ed.). Academic Press, New York, pp. 81-87
- Strong D. R., Lawton J. H. and Southwood T. R. E. (1984) Insect on Plants. Blackwell Scientific Publications, Oxford.
- Trichilo, P. J. and Leigh, T. F. (1986) Predation on spider mite eggs by the Western Flower Thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), an opportunist in a cotton agroecosystem. *Environ. Entomol.* 15: 821-825

Fig. 1-a Preparation for a choice test using *C. japonica* leaflets. Leaflets with broken lines were removed before the experiment. The petiole of leaflet in a pair was banded with wet cotton to prevent *T. kanzawai* from escaping, while the other leaflet served as a control

Fig. 1-b Experimental setup for a choice test using hornworms. We removed wet cotton from the petiole and introduced a hornworm at the bottom edge of the *C. japonica* compound leaf

Fig. 2-a Preparation for a choice test using *P. trifoliata* leaflets. Leaflets with broken lines were removed before the experiment. The petiole of one leaflet in a pair was banded with wet cotton to prevent *P. citri* from escaping, while the other leaflet served as a control

Fig. 2-b Experimental setup for the choice test using a swallowtail caterpillar. The wet cotton was removed from the petiole and the caterpillar was introduced at the bottom edge of the *P. trifoliata* compound leaf

Fig. 3 Proportion of *T. kanzawai* consumed when attacked by a hornworm

Fig. 4 Preference of caterpillars for mite-infested vs. uninfested leaflets (a: NS; $P = 0.36$, b: NS; $P > 0.99$, c: NS; $P = 0.22$)

Fig. 5 Proportion of *P. citri* consumed when attacked by a *P. xuthus* caterpillar

Table 1 Results of the Wald test for the effects of populations and developmental stages on the survival of *T. kanzawai* when attacked by a hornworm

Fig. 1

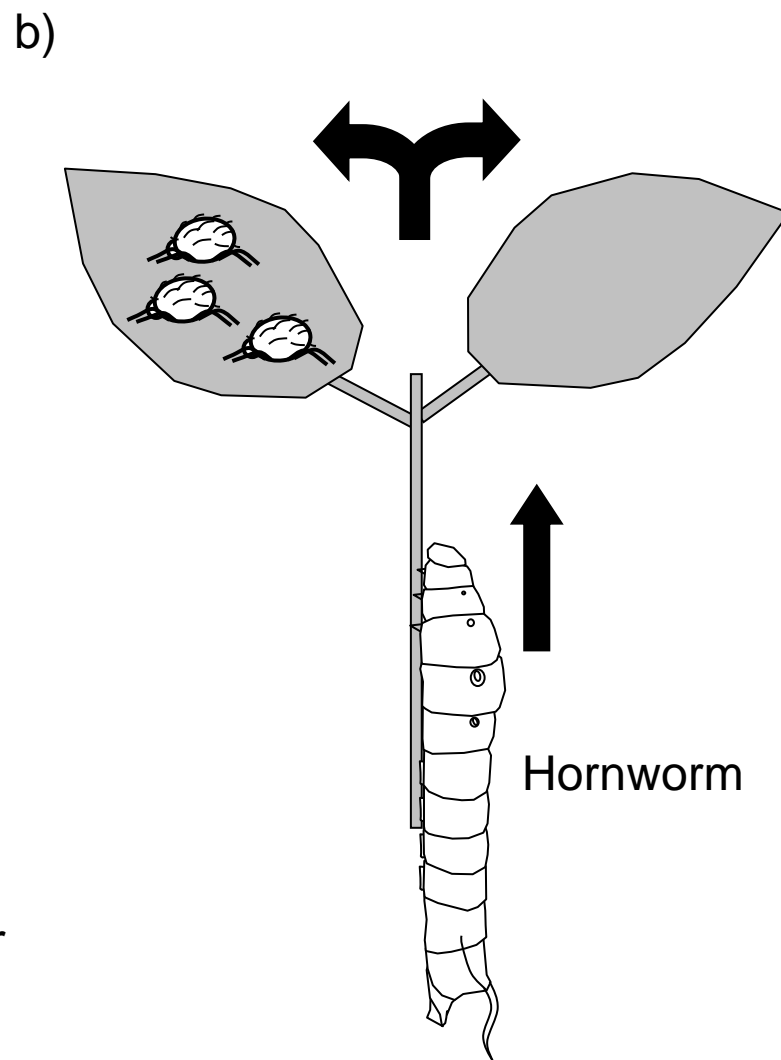
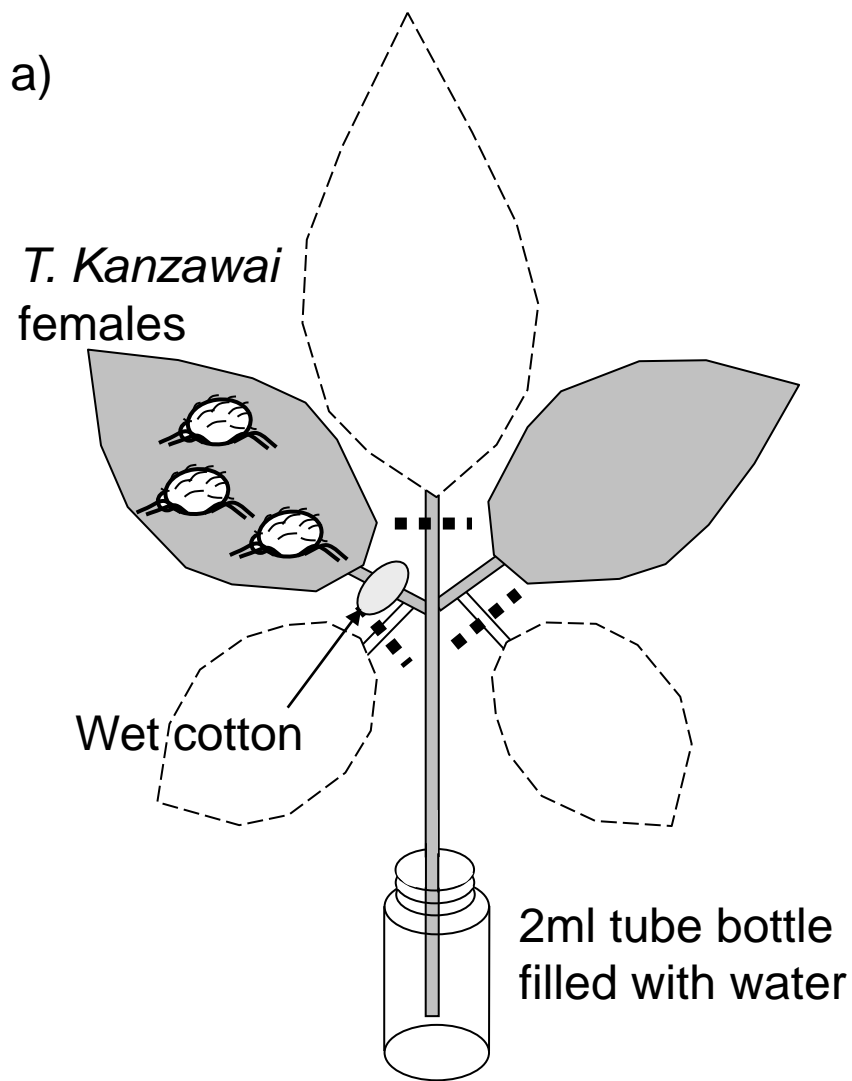


Fig. 2

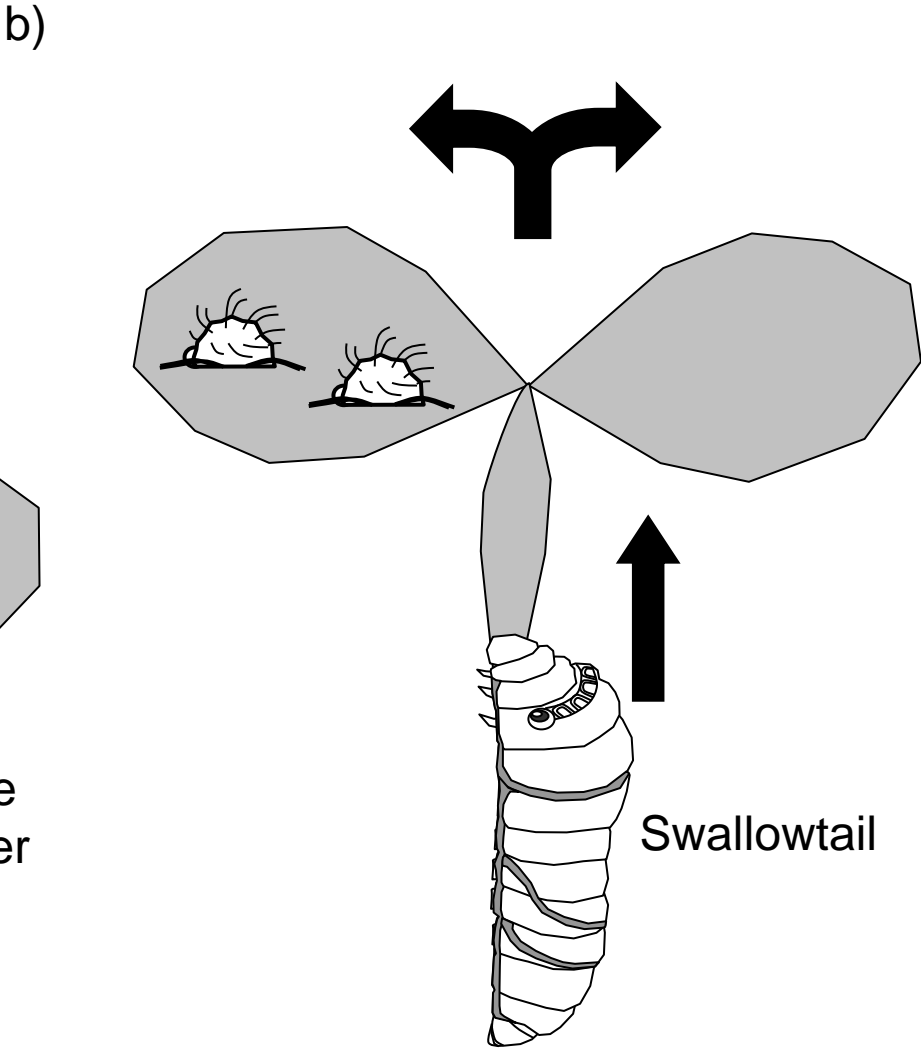
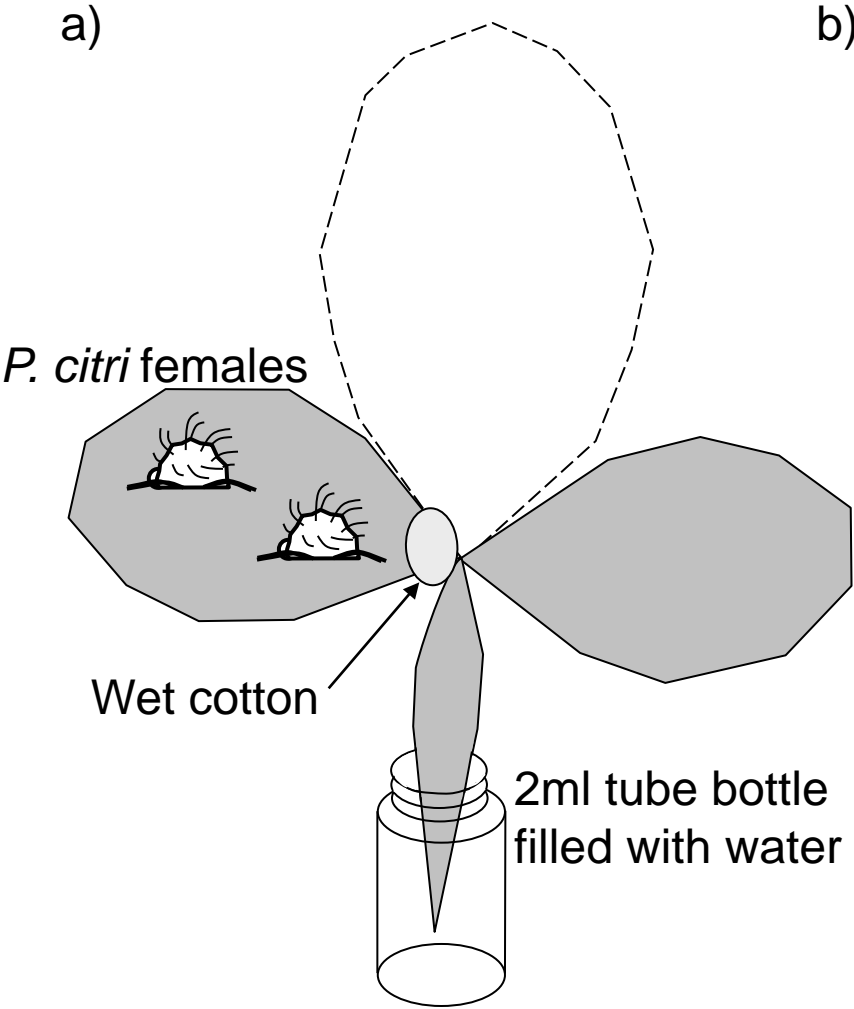


Fig. 3

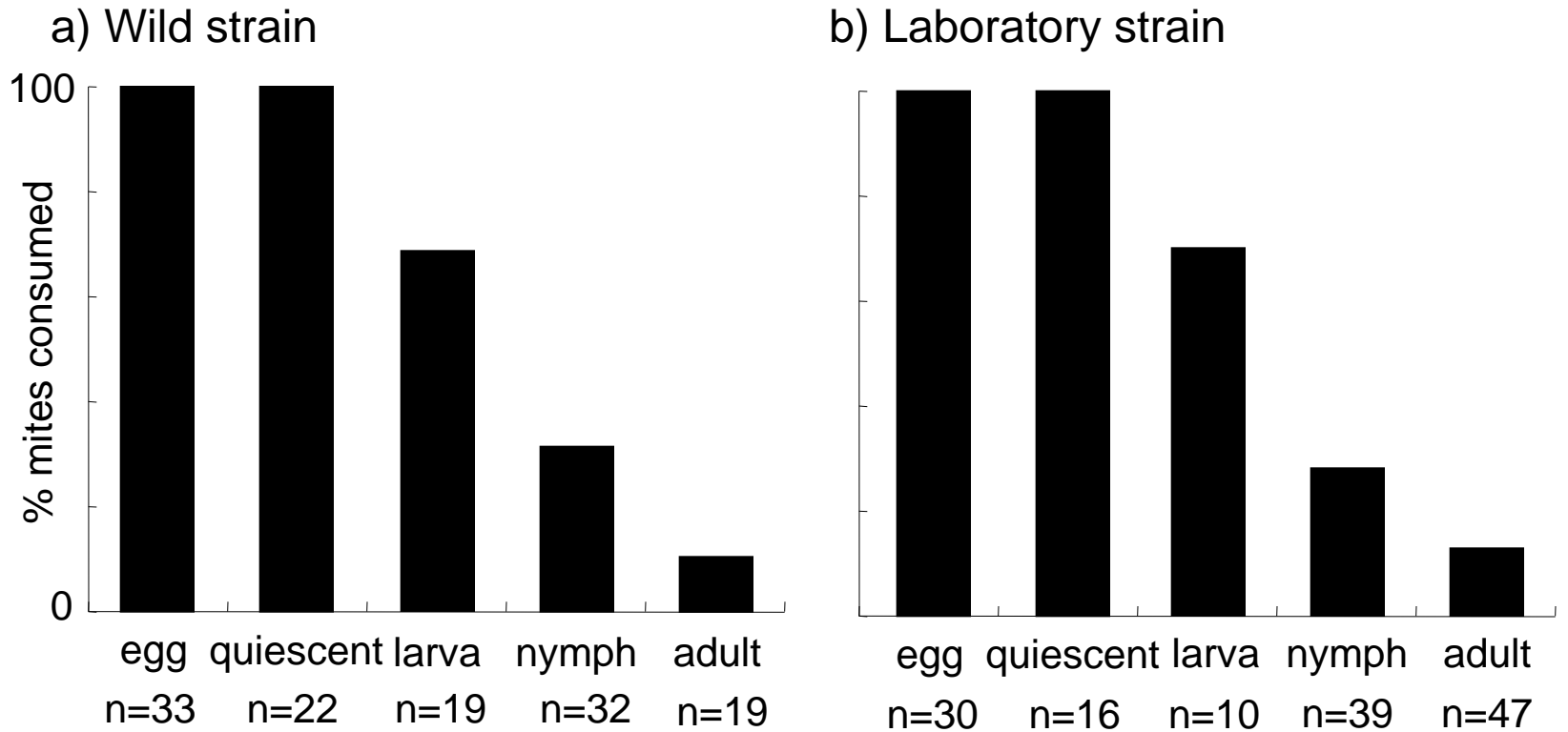


Fig. 4

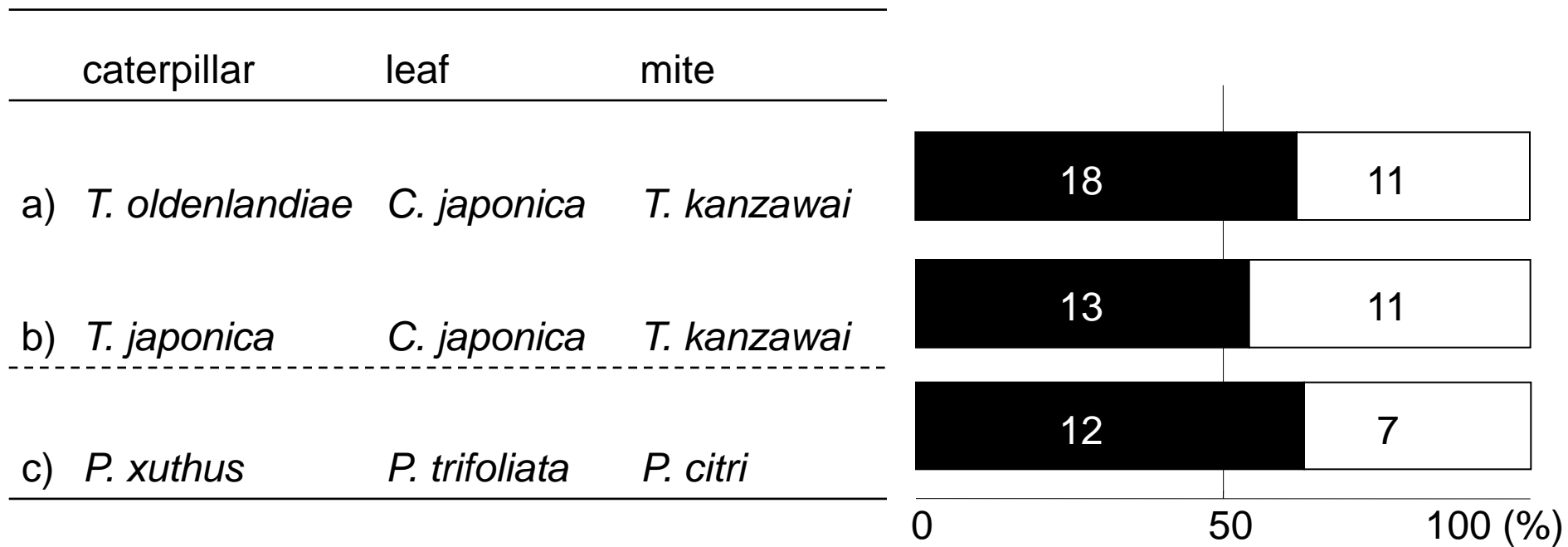


Fig. 5

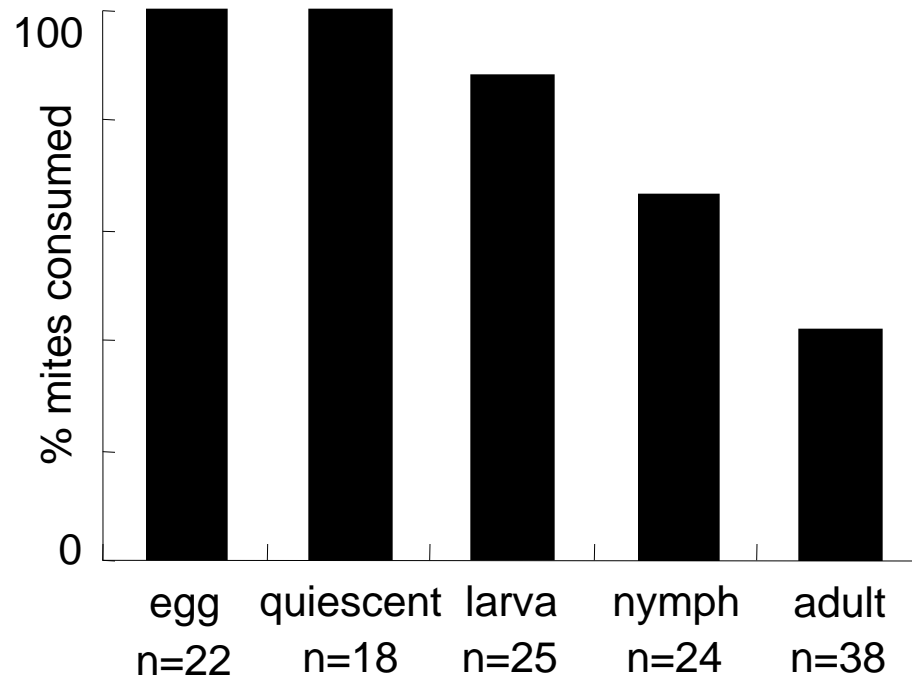


Table 1

Factor	df	Wald χ^2	<i>P</i>
Population (Wild/ Laboratory)	1	0.0035	0.9531
Stage (larva/ nymph/ adult)	2	22.592	<i>P</i> <0.001
Population \times stage	2	0.2171	0.8971