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Predatory mites protect own eggs against predators

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Abstract

Predators frequently compete with other species for prey but can also interact by preying on each other's vulnerable stages. Because eggs and juveniles are more vulnerable to this intraguild predation than adults, their survival will depend on maternal strategies to reduce predation risk. Recently, we reported that adult female predatory mites *Gynaeseius liturivorus* Ehara (Acari: Phytoseiidae) reduce intraguild predation on their eggs by remaining at oviposition sites, thus deterring the egg predators. In addition, they avoid oviposition close to eggs laid by conspecific females. We therefore expected that adult female *G. liturivorus* protect their own eggs better against these egg predators than eggs of other females. This was tested using juveniles of the predatory mite *Neoseiulus californicus* McGregor (Acari: Phytoseiidae) as egg predators and the western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae), as the shared prey. When *G. liturivorus* eggs were kept with their mothers, the presence of juvenile egg predators did not affect the survival of eggs. However, when *G. liturivorus* eggs were kept with females that were not their mothers, the mortality of eggs in the presence of juvenile egg predators increased. When adult female *G. liturivorus* were guarding their eggs, they killed a similar number of juvenile egg predators as females that were not kept with their eggs. Hence, adult female *G. liturivorus* protect their eggs by remaining close to their eggs.

Introduction

When animal species compete for the same food resources, the predation that occurs between them is termed intraguild (IG) predation (Polis et al., 1989; Polis & Holt, 1992; Arim & Marquet, 2004). To reduce the risk of IG predation, IG prey may avoid places with IG predators (Moran & Hurd, 1994; Magalhães et al., 2005; Çakmak et al., 2006; Velasco-Hernández et al., 2013), use refuges (Moran & Hurd, 1994; Ferreira et al., 2011), retain the eggs inside their bodies (Montserrat et al., 2007), or reduce foraging activity (Wissinger & McGrady, 1993; Okuyama, 2002). Because juveniles and eggs are usually more vulnerable to predation than adults, IG-prey mothers are expected to select oviposition sites with lower risk of IG predation

to increase the survival of their offspring (Almohamad et al., 2010; Choh et al., 2010; van der Hammen et al., 2010; Walzer & Schausberger, 2011). However, IG predators may have a similar preference for oviposition sites as IG prey (Pumariño et al., 2011; Huang & Pike, 2012; Choh et al., 2015; Saitoh & Choh, 2018a). Our recent study showed that IG-prey mothers protected their eggs against IG predators sharing the same oviposition sites (Saitoh & Choh, 2018a).

Parental and maternal care of eggs is observed in a wide range of taxa (Royle et al., 2012) and improves the survival of offspring by protection against predators (Evans, 1998; Croshaw & Scott, 2005; Requena et al., 2009), by grooming and incubation (Aubret et al., 2005; Munguía-Steyer et al., 2008; Boos et al., 2014). However, prey individuals that take care of their eggs may themselves be more susceptible to attack by predators than those that do not exhibit such behavior (Reguera & Gomendio, 1999; Li & Jackson, 2003; Suzuki & Futami, 2018). Consequently, parental care

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usually comes with costs, so may go at the expense of future reproduction (Tallamy & Denno, 1982; Dijkstra et al., 1990; Smith & Wootton, 1994; Balshine-Earn, 1995). According to the theory of inclusive fitness, parents should take care of genetically related eggs and young to increase their fitness (Hamilton, 1964; Foster et al., 2006; Nowak, 2006). Here, we tested whether IG-prey mothers protect eggs laid by conspecific females (i.e., a type of alloparental care) (Riedman, 1982) against IG predators or protect their own eggs better than eggs from conspecific females using two predatory mite species.

Gynaeseius liturivorus Ehara (Acari: Phytoseiidae) is a predatory mite that feeds on all stages of western flower thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae), whereas the other predatory mite, *Neoseiulus californicus* McGregor (Acari: Phytoseiidae) only feeds on thrips larvae (Y Choh & F Saitoh, pers. obs.). Adults and larger juveniles of the two mite species reciprocally prey on each other's eggs and smaller juveniles. Because the attack rate of *N. californicus* on eggs of *G. liturivorus* is higher than the reverse (F Saitoh, pers. obs.), we used *N. californicus* here as egg predator of *G. liturivorus*. The two mite species are observed on the same plants, including soybeans (Mori et al., 2008), and eggs of both species are found on similar plant structures such as leaf veins and hairs (Y Choh, pers. obs.). Thus, eggs of *G. liturivorus* are likely to suffer from egg predation by *N. californicus*. In turn, adult *G. liturivorus* can attack juvenile *N. californicus* (Saitoh & Choh, 2018a). We recently showed that intraguild predation on *G. liturivorus* eggs by *N. californicus* was reduced when adult female *G. liturivorus* remained at their oviposition sites (Saitoh & Choh, 2018a), suggesting that they guard their eggs. We have also shown that adult female *G. liturivorus* avoid oviposition sites of conspecific females when alternative oviposition sites are available (Saitoh & Choh, 2018b), suggesting some mechanism of kin recognition. However, oviposition sites are often scarce under natural conditions, and several females of *G. liturivorus* and their eggs are often observed on the same plant leaf. The question then is, whether females specifically guard their own eggs or also eggs of other females. Besides by the intraguild predator *N. californicus*, the eggs of *G. liturivorus* in our study system may also be attacked by thrips larvae (Janssen et al., 2003; Choh et al., 2017) and conspecific adult females (i.e., cannibalism). We therefore first assessed whether predation by *N. californicus* was the major mortality factor of *G. liturivorus* eggs. Subsequently, the survival of *G. liturivorus* eggs was investigated in the presence and absence of IG predators and conspecific adult females, focusing on kinships between eggs and adult females of *G. liturivorus*.

Materials and methods

Plants and arthropods

Kidney bean plants, *Phaseolus vulgaris* cv. Nagauzura (Fabaceae), were grown in soil in pots (8.5 cm diameter, 7 cm high) in a greenhouse at 25 ± 2 °C, $60 \pm 10\%$ r.h., and L16:D8 h photoperiod. For experiments, we used the primary leaves of the plants 10–12 days after sowing the seeds.

Western flower thrips were obtained in 2011 from Sumika Techno Service (Takarazuka, Japan). They were maintained on kidney bean leaf discs (6 cm diameter) placed on water-saturated cotton wool in Petri dishes (9 cm diameter, 2 cm high) and supplied with ample alder pollen (*Alnus sieboldiana* Matsum., Betulaceae). Pollen was collected from alder plants located on the campus of Chiba University and treated as described by Montserrat et al. (2006). We used first-instar thrips that had emerged from leaf discs within 24 h for experiments.

Gynaeseius liturivorus were collected in October 2012 from green onion fields at Chiba City, Japan. They were maintained on kidney bean leaves with thrips larvae as food and were offered new leaves 3× per week.

We obtained *N. californicus* in 2010 from Arysta LifeScience (Tokyo, Japan). To exclude effects of oviposition by adult female *N. californicus* on the behavior of adult female *G. liturivorus*, we used larvae of *N. californicus* (within 24 h after hatching) for all experiments. Larvae changed into protonymphs during experiments. Because younger stages of *N. californicus* are less capable of capturing mobile prey (i.e., thrips larvae) than are older predator stages, newly emerged protonymphs were expected to prefer attacking immobile prey (i.e., IG-prey eggs) to thrips larvae. Hence, larvae and protonymphs of *N. californicus* were used as IG predators of *G. liturivorus* eggs in this study. They were reared on detached kidney bean leaves that were heavily infested with two-spotted spider mites, *Tetranychus urticae* Koch (Acari: Tetranychidae), which is a superior prey species for this predator (Choh et al., 2017). Leaves with these prey were added to the culture every 2 days. *Tetranychus urticae* were obtained in 2010 from a culture maintained at the National Institute of Agrobiological Sciences (Tsukuba, Japan) and reared on kidney bean plants. Cultures of all arthropod species were maintained in separate incubators (25 ± 2 °C, $60 \pm 10\%$ r.h., L16:D8), and individuals of the proper stage were randomly selected from the cultures for experiments. We conducted all experiments in a climate-controlled room (25 ± 2 °C, $60 \pm 10\%$ r.h., L16:D8).

Predation risk of *Gynaeseius liturivorus* eggs

To investigate predation of *G. liturivorus* eggs, we assessed the number of *G. liturivorus* eggs in the presence of thrips larvae, adult *G. liturivorus* (potential cannibals), or juvenile *N. californicus*. Leaf discs (20 mm diameter) were used as patches for predatory mites. Under laboratory conditions, adult female *G. liturivorus* prefer to oviposit on pieces of plastic rather than on leaf discs (Saitoh & Choh, 2018a), and we therefore offered clear plastic discs (6 mm diameter) as oviposition substrates on top of the leaf discs. First, an adult female *G. liturivorus* was introduced onto such a leaf disc with a plastic disc and kept with 20 first-instar thrips for 24 h. Plastic discs on which seven eggs had been laid by a female mite were subsequently put on another leaf disc of the same size as the above. Then, either 20 first-instar thrips, two larvae of *N. californicus*, the mother of the *G. liturivorus* eggs, or an adult conspecific female that did not produce the eggs (hereinafter referred to as other females) were released onto the disc. The numbers of thrips larvae and *N. californicus* were based on our previous studies (Saitoh & Choh, 2018a). As control, a plastic disc with eggs was placed on a leaf disc without any potential predator. The number of *G. liturivorus* eggs was assessed 24 h later, and each treatment had 21 replicates.

Protection of *Gynaeseius liturivorus* eggs by adult females

We investigated whether the presence of adult female *G. liturivorus* differently affected the survival of conspecific eggs or their own eggs. Plastic discs with seven *G. liturivorus* eggs were obtained as described above. Subsequently, they were placed on a new leaf disc (20 mm diameter) and either the mother of the eggs or an unrelated conspecific female (other females) was released onto the leaf disc together with two *N. californicus* larvae. In addition, 20 first-instar thrips were placed on the leaf disc, serving as prey for both mite species. Another treatment without adult female *G. liturivorus* on the leaf disc, and one without juvenile *N. californicus* served as controls. The numbers of *G. liturivorus* eggs on the plastic discs and the survival of the juvenile *N. californicus* and thrips larvae were assessed 24 h later. Adult female *G. liturivorus* oviposited during the experiment, and we assessed the total numbers of eggs without discriminating between eggs that had been laid before the experiment and those laid during the experiment. Each treatment was replicated 20×.

Statistical analysis

The effects of the various predators on the numbers of *G. liturivorus* eggs were compared with a GLM with a quasi-Poisson error distribution (log link). Contrasts among treatments were assessed with pairwise comparisons with Tukey corrections with the package emmeans (Lenth,

2019). The effects of the presence of juvenile *N. californicus* and adult female *G. liturivorus* on the numbers of eggs and the survival of thrips larvae were analysed with a GLM with a quasi-Poisson error distribution (log link) with the presence of female *G. liturivorus* (three levels: mothers, other females, or none) and *N. californicus* (two levels: present or absent) and their interaction as factors. Survival of juvenile *N. californicus* was analysed with a similar model with the presence of female predators as factor. Contrasts were assessed as above. All statistical analyses were performed in R v.3.6.1 (R Core Team, 2019).

Results

Predation risk of *Gynaeseius liturivorus* eggs

The number of *G. liturivorus* eggs was significantly affected by the presence of arthropods kept with the eggs (GLM: $F_{4,100} = 89.5$, $P < 0.0001$). The presence of thrips larvae did not significantly affect the number of *G. liturivorus* eggs (Figure 1), but the presence of juvenile *N. californicus* significantly reduced the number of eggs. Adult female *G. liturivorus* oviposited during the experiment, and the number of eggs was significantly higher with females than in the other treatments, irrespective of the relationship of the females with the eggs (Figure 1). Egg cannibalism by adult female *G. liturivorus* was not observed during experiments, which was verified by the absence of remains of preyed eggs.

Protection of *Gynaeseius liturivorus* eggs by adult females

The number of *G. liturivorus* eggs was affected by the interaction between the presence of juvenile *N. californicus* and the presence of adult female *G. liturivorus* (GLM: $F_{2,126} = 5.47$, $P = 0.0053$). The release of adult female *G. liturivorus* resulted in an increased number of eggs because

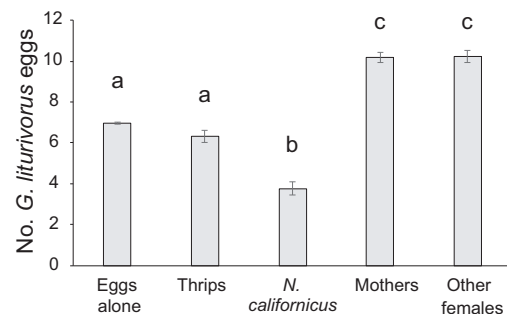


Figure 1 Mean (\pm SEM) number of *Gynaeseius liturivorus* eggs when being kept alone or with thrips larvae, a juvenile *Neoseiulus californicus*, the mothers of the egg, or other females. Means capped with different letters are significantly different (Contrasts after GLM: $P < 0.05$).

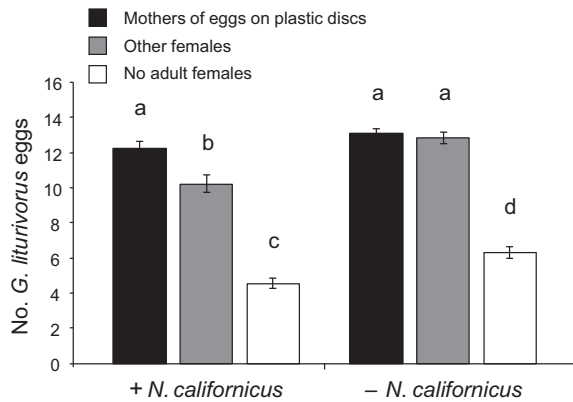


Figure 2 Mean (\pm SEM) number of *Gynaeseius liturivorus* eggs in the absence or presence of juvenile *Neoseiulus californicus* egg predators when being kept with the mothers of the eggs, with other females, or without an adult female *G. liturivorus*. Means capped with different letters are significantly different (Contrasts after GLM: $P < 0.05$).

of oviposition occurring during the experiment (Figure 2, white bars vs. black and grey bars). As expected, juvenile *N. californicus* reduced the number of *G. liturivorus* eggs in the absence of an adult female *G. liturivorus* (Figure 2, white bars), and in the presence of other females (Figure 2, grey bars), but not in the presence of the mothers of the eggs (Figure 2, black bars). In the presence of juvenile *N. californicus*, the number of *G. liturivorus* eggs together with other females was higher than that without conspecific females (Figure 2, left grey and white bars), but lower than that together with mothers of the eggs (Figure 2, left black bar). In the absence of juvenile *N. californicus*, the number

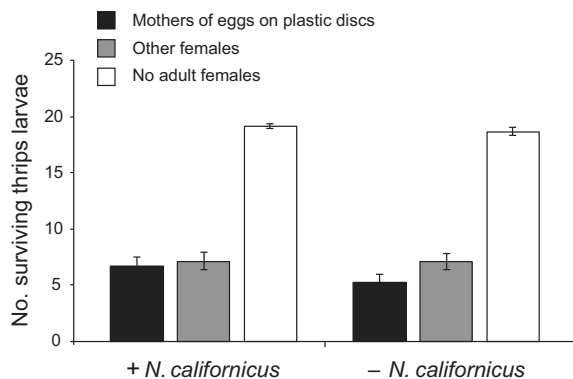


Figure 3 Mean (\pm SEM) number of surviving thrips larvae in the absence or presence of juvenile *Neoseiulus californicus* when being kept with the mother of *Gynaeseius liturivorus* eggs, with other females, or without an adult female *G. liturivorus*.

of *G. liturivorus* eggs together with their mothers did not differ from that together with other females (Figure 2, right black and grey bar).

The number of surviving thrips larvae was affected by the presence of an adult female *G. liturivorus* (Figure 3; GLM: $F_{2,129} = 144.3$, $P < 0.001$), but not by the presence of juvenile *N. californicus* (GLM: $F_{1,128} = 0.92$, $P = 0.34$) or by the interaction between these two factors (GLM: $F_{2,126} = 0.94$, $P = 0.39$). Survival of thrips larvae was not affected by the relatedness of the adult female *G. liturivorus* with the eggs (Figure 3).

Not all juvenile *N. californicus* were found alive on leaf discs due to natural mortality, also in the absence of adult female *G. liturivorus* (Figure 4). The presence of adult female *G. liturivorus* affected the number of surviving juvenile *N. californicus* (Figure 4; GLM: $F_{2,63} = 3.25$, $P = 0.045$). The survival of juvenile *N. californicus* in the presence of mothers of the eggs was lower than that in the absence of *G. liturivorus*, but did not differ from that in the presence of other females (Figure 4).

Discussion

Predation by juvenile *N. californicus* was an important mortality factor of *G. liturivorus* eggs when the mother of these eggs was not present. In the presence of the mothers of the eggs, egg predation was difficult to measure because the females added new eggs during the experiment, and it is unclear how many of these new and old eggs were killed. However, the total numbers of eggs in the presence of the mother of the eggs did not differ with the presence or absence of the egg predator, suggesting that egg predation was very low or absent (Saitoh & Choh, 2018a). In

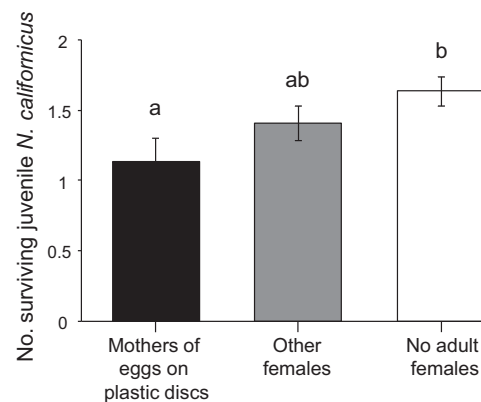


Figure 4 Mean (\pm SEM) number of surviving juvenile *Neoseiulus californicus* when being kept with the mother of *Gynaeseius liturivorus* eggs, with other females, or without an adult female *G. liturivorus*. Means capped with different letters are significantly different (Contrasts after GLM: $P < 0.05$).

contrast, when a female that was not related to the initial eggs was present, fewer eggs were found, suggesting increased predation of the eggs by *N. californicus*. Hence, females protect their own eggs against juvenile egg predators more effectively than eggs of other females. Further study is needed into the effects of developmental stages and gender of *N. californicus* on egg protection by adult female *G. liturivorus*.

In an earlier study with the same experimental set-up, we showed that adult female *G. liturivorus* spend most of their time close by their own eggs, that juvenile *N. californicus* spent less time on the plastic discs with eggs when the mother of the eggs was present than when she was absent, and that these egg predators consumed *G. liturivorus* eggs only when the mothers of the eggs were not close to their eggs (Saitoh & Choh, 2018a). This suggests that the main effect of the presence of the mothers is deterrence of the egg predators. Hence, females might have spent less time close to eggs of other females than to their own eggs in the present study. Indeed, *G. liturivorus* females are known to prefer ovipositing close to their own eggs rather than close to eggs of other females (Saitoh & Choh, 2018b), and are known to discriminate between own eggs and those of other females (Saitoh et al., 2020).

An alternative explanation for the increased numbers of eggs in the presence of the mothers is that these mothers kill more egg predators, resulting in less egg predation. Although the difference in survival of *N. californicus* between the treatment with mothers vs. other females was not significant, there was a trend of lower survival of the egg predators in the presence of the mothers. Assuming that the per capita predation rate of *N. californicus* by the adult *G. liturivorus* is constant through time, the average densities of *N. californicus* during the experiment would be 1.53 individuals in the presence of the mothers and 1.69 in the presence of other females. Assuming subsequently that the per capita egg predation rate by these egg predators is also constant through time, the predation rate per individual should be more than $3\times$ as low in the presence of the mothers than in the presence of other females (0.049 vs. 0.189 eggs per individual per day, respectively). This shows that the differences in egg numbers with the mothers vs. other females are unlikely to be explained by the increased killing of the egg predators by mothers but probably by deterrence of the egg predators by the mothers.

Because the adult *G. liturivorus* oviposited during the experiment, the numbers of own eggs of the females present increased during the experiment, also for the other females that did not produce the eggs initially present. It is therefore expected that these other females also spent increasing amounts of time close to the eggs over the course of the experiment. This will have affected the predation of

the eggs; hence, the differences in numbers of eggs between the treatments with *N. californicus* observed are probably an underestimation of the true effect of kin-relatedness on egg guarding and its effects on egg predation. If other females would have been offered another oviposition site, they would probably oviposit there (Saitoh & Choh, 2018b) and guard the eggs present from the beginning significantly less.

In theory, the presence of juvenile *N. californicus* could have resulted in lower numbers of thrips larvae, thus less food for the *G. liturivorus* females, resulting in lower oviposition rates by the latter. However, the densities of thrips larvae did not differ between treatments with and without *N. californicus*; hence, this possibility can safely be ruled out.

When adult female *G. liturivorus* encounter unfamiliar eggs at an oviposition site, this indicates the presence of other females. In fact, several individual females of *G. liturivorus* are often observed within the same patch, for example on folded leaves in fields of green onions and soybeans. When animals live in groups, they may be genetically related (de Ruiter & Geffen, 1998; Archie et al., 2006; Lee et al., 2010). Under such conditions, an individual is likely to benefit from the behaviors of other individuals (Pusey & Packer, 1994; Griesser et al., 2006; Griesser & Suzuki, 2016), as predicted by the inclusive fitness theory (Hamilton, 1964). Although adult female *G. liturivorus* did not protect eggs of other females against juvenile *N. californicus* as effectively as they did their own eggs, kinship among adult females in a group might affect the survival of their eggs. For example, long-tailed tits (*Aegithalos caudatus* L.) that have failed breeding prefer to help caring for kin over non-kin chicks when offered a choice (Russell & Hatchwell, 2001), resulting in an increased survival of offspring (Hatchwell et al., 2004). It is worth testing whether kin individuals of adult female *G. liturivorus* cooperatively reduce the risk of predation of their offspring as a form of alloparental care (Riedman, 1982).

In classic predator-prey systems, several studies have reported that adult prey protect kin juveniles better against predators than non-kin juveniles (Sherman, 1977; Griesser & Nystrand, 2009; Griesser & Suzuki, 2016). This study shows that adult female *G. liturivorus* protected their own eggs better against IG predators than eggs of other females, possibly by deterring juvenile IG predators. Protection of offspring by intraguild prey as described here, weakens the strength of intraguild predation and could facilitate the coexistence of intraguild predators and intraguild prey, whereas such coexistence is not predicted by most theoretical studies (Holt & Polis, 1997; Mylius et al., 2001). Future studies on intraguild interactions should pay more attention to

defensive behavior of adults, also in species that are not traditionally considered to have maternal care.

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