Animal Behaviour 140 (2018) 49-55

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Do intraguild prey protect their eggs from intraguild predators that share their oviposition site?

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ARTICLE INFO

Article history: Received 29 August 2017 Initial acceptance 1 November 2017 Final acceptance 9 March 2018

MS. number: 17-00697R

Keywords: antipredator behaviour intraguild predation maternal care oviposition preference predator-prey interactions Intraguild (IG)-prey prefer to oviposit at sites with a low IG-predation risk of their offspring. However, IG-predators sometimes show oviposition preferences similar to those of IG-prey. In such cases, IG-prey eggs might need protection against IG-predators to survive. We tested this possibility using a system that consisted of an IG-prey, the predatory mite Gynaeseius liturivorus, and an IG-predator, the predatory mite Neoseiulus californicus. Both mite species feed on larvae of the western flower thrips, Frankliniella occidentalis, as a shared food source. When offered plastic discs as substrates for oviposition, both mite species preferred to lay eggs on the discs, regardless of the presence of heterospecifics. Subsequently, we examined G. liturivorus egg survival in the presence of only conspecific mothers or N. californicus, and the presence and absence of both mite species. The survival of G. liturivorus eggs was significantly reduced when kept with only N. californicus, but this reduction was not found in the presence of both G. liturivorus and N. californicus. These results indicate that G. liturivorus mothers improved the survival of the eggs in the presence of *N. californicus*. Behavioural observation revealed that adult female *G. liturivorus* mostly remained on the plastic discs with their own eggs during experiments. Furthermore, the presence of G. liturivorus mothers reduced the residence time of N. californicus on plastic discs with G. liturivorus eggs, whereas the residence time of G. liturivorus mothers was not affected by the presence of N. californicus. We conclude that mothers of *G. liturivorus* are able to increase the survival of their eggs by deterring IGpredators.

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Intraguild (IG) predation occurs between species that share the same food (Arim & Marquet, 2004; Polis, Myers, & Holt, 1989; Polis, Winemiller, & Pimm, 1996). Theories predict that IG-predators and IG-prey are only able to coexist when the IG-prey is superior in terms of competition for resources shared with the IG-predator (Holt & Polis, 1997; Mylius, Klumpers, de Roos, & Persson, 2001). Nevertheless, IG-predation is commonly observed in nature (Polis et al., 1989). This conflict between theory and observation could be explained by the effects of several factors on IG-interactions, such as habitat structure (Janssen, Sabelis, Magalhães, Montserrat, & Van der Hammen, 2007), extraguild prey density (Lucas & Rosenheim, 2011), shared resources, temperature (Sentis, Hemptinne, & Brodeur, 2014), and the stage structures of IG-predators and IG-prey (Montserrat, Magalhães, Sabelis, De Roos, & Janssen, 2012). Investigation of the factors that affect the

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strength of IG-predation is crucial for elucidating the coexistence of IG-predators and IG-prey in nature.

IG-prey avoid places with IG-predators (Cakmak, Janssen, & Sabelis, 2006; Moran & Hurd, 1994; Velasco-Hernández, Ramirez-Romero, Cicero, Michel-Rios, & Desneux, 2013), and decrease their activity (Okuyama, 2002; Wissinger & McGrady, 1993) and use refuges (Ferreira, Cunha, Pallini, Sabelis, & Janssen, 2011; Moran & Hurd, 1994) to escape IG-predators. However, juveniles and eggs are more vulnerable to predation than adults. Therefore, mothers of IG-prey tend to select oviposition sites with a lower IG-predation risk for offspring (Amiri-Jami, Sadeghi, Gilbert, Moravvej, & Asoodeh, 2016: Choh, Van der Hammen, Sabelis, & Janssen, 2010: Rojas, 2014: Van der Hammen, De Roos, Sabelis, & Janssen, 2010: Walzer & Schausberger, 2011). However, some IG-predators show an oviposition site preference similar to that of the IG-prey (Choh, Sabelis, & Janssen, 2015; Huang & Pike, 2012; Pumariño, Alomar, & Lundgren, 2011); in this case, eggs of IG-prey would be exposed to IG-predation. Parental or maternal care, which is a potential way to increase survival of eggs in the presence of predators, occurs in several animal species (Royle, Smiseth, & Kölliker, 2012; Seiter & Schausberger, 2015; Wong, Meunier, & Kölliker, 2013). For







https://doi.org/10.1016/j.anbehav.2018.04.005

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example, the burrower bug, *Adomerus triguttulus*, attends to the egg mass for protection against predators (Nakahira & Kudo, 2008). However, no studies have examined parental or maternal care in IG-interactions. Here, we studied whether and how IG-prey protect their eggs from IG-predators.

The system used in this study consisted of the western flower thrips. Frankliniella occidentalis and two predatory mite species. Gynaeseius liturivorus and Neoseiulus californicus. Gynaeseius liturivorus feeds on all developmental stages of thrips, whereas N. californicus only feeds on thrips larvae. Both mite species are involved in reciprocal IG-predation, in which both species consume the juveniles and eggs, but not the adults, of the other species. Because IG-predation by N. californicus is observed more frequently than IG-predation by G. liturivorus (F. Saitoh, personal observation), we used N. californicus as IG-predators and G. liturivorus as IG-prey in this study. The two predatory mite species co-occur on the same crop plants, such as soy bean (Mori, Takagi, Kohjimoto, Gotoh, & Kobayashi, 2008), and the eggs of both species are found on similar leaf structures, such as leaf veins and hairs. Although cooccurrence of these mite species has not been investigated in nature, N. californicus is likely to encounter eggs of G. liturivorus in crop fields. Adult female G. liturivorus are often found close to conspecific eggs (F. Saitoh, personal observation). Consequently, we tested whether the presence of adult female G. liturivorus led to increased survival of eggs under IG-predation threat. First, to confirm whether G. liturivorus eggs are likely to be exposed to IGpredation, we examined oviposition site preferences of the two predatory mite species in the presence and absence of heterospecifics by offering artificial substrates for oviposition. Subsequently, we investigated whether the survival of G. liturivorus eggs was affected by the presence of conspecific adult females, by manipulating combinations of the two predatory mite species. Although cannibalism could occur among G. liturivorus juveniles or between juveniles and eggs, adult females do not attack the eggs (Y. Choh and F. Saitoh, personal observation). Therefore, the mortality of G. liturivorus eggs is not affected by the presence of conspecific adult females. In addition, to clarify possible mechanisms responsible for differences in the survival of G. liturivorus eggs, we observed behaviours of the two predatory mite species.

METHODS

Plants and Arthropods

Kidney bean, *Phaseolus vulgaris* cv. Nagauzura, plants were grown in soil in a greenhouse at 25 ± 1 °C and $60 \pm 10\%$ relative humidity (RH), under a photoperiod of 16:8 h light:dark. We used the primary leaves of the bean plants 10–12 days after sowing the seeds.

Western flower thrips were purchased from Sumika Techno Service Corporation (Takarazuka, Japan) in 2011 and reared on kidney bean plants. Gynaeseius liturivorus were collected from green onions in Matsudo City, Japan in April 2016; they were maintained on kidney bean leaves with several thrips larvae and offered new leaves twice per week. Two-spotted spider mites, Tetranychus urticae, were obtained from a culture maintained at the National Institute of Agrobiological Sciences (Tsukuba, Japan) in 2010 and reared on kidney bean plants. Neoseiulus californicus were purchased from Arysta LifeScience (Tokyo, Japan) in 2010; we reared these predatory mites on detached kidney bean leaves that were heavily infested with T. urticae and added leaves to the culture every 2 days. Cultures of the four arthropod species were separately maintained in incubators (25 ± 2 °C, 50-70% RH, 16:8 h light:dark), and individuals were randomly selected from the cultures to be used for the following experiments. All experiments were conducted in a climate-controlled room (25 ± 2 °C, 50–70% RH, 16:8 h light:dark).

Oviposition Preferences of the Mites

To clarify whether the oviposition sites of the two predatory mite species could potentially overlap in nature, we investigated their oviposition site preferences. As a substrate for oviposition, a clear plastic disc (diameter 6 mm) was placed at the centre of a leaf disc (diameter 20 mm) on water-saturated cotton wool in a petri dish (diameter 9 cm; depth 2 cm). Although leaf hairs and veins are preferred as oviposition sites by the two predatory mites, their sizes and shapes differ between leaves and plants. To avoid these oviposition site differences affecting the behaviour of the two mite species, we offered them plastic discs of the same size and shape. An adult female of either G. liturivorus or N. californicus was introduced onto the leaf disc with a fine paint brush along with 20 first-instar thrips larvae. For the experiments, we used gravid adult female G. liturivorus and N. californicus 8-12 and 10-14 days after hatching, respectively. To test the effects of the presence of heterospecifics on oviposition site preferences of the other mite species, an adult female of each mite species (i.e. two individual mites) was released as described above. The sequence of release of the two species was switched for each replication. The number and location (plastic or leaf discs) of the eggs were determined 24 h after introduction under a binocular microscope. Under these conditions, surviving thrips larvae remained on the leaf discs until the end of the experiments. The eggs of G. liturivorus (major axis 0.23 ± 0.003 mm; minor axis 0.17 ± 0.002 mm) were larger than *N. californicus* eggs (major axis 0.19 ± 0.002 mm; minor axis 0.14 ± 0.001 mm; N = 10 for both species), which facilitated species identification of the eggs.

Each treatment was replicated 30 times. The numbers of eggs of each mite species were compared with a two-way repeated measures ANOVA (the effects of oviposition sites and heterospecifics on the number of eggs). All statistical analyses were performed using R version 3.3.2 (R Development Core Team, 2016).

Survival of G. liturivorus Eggs

The survival of *G. liturivorus* eggs was examined after manipulating the presence of the two predatory mite species. We prepared leaf discs and clear plastic discs as described above. An adult female *G. liturivorus* was placed onto a leaf disc with 20 first-instar thrips larvae and a plastic disc for 24 h. Then, we counted the *G. liturivorus* eggs laid on the plastic disc. Subsequently, we moved the plastic disc with eggs onto a new leaf disc and released 20 first-instar thrips larvae.

To test IG-predation on eggs of *G. liturivorus*, we first introduced three juvenile *N. californicus* (< 24 h after hatching) onto the leaf discs. Because the presence of adult female *N. californicus* did not affect total oviposition of adult female *G. liturivorus* (see Results), *G. liturivorus* eggs might not be attacked by heterospecific adults. Therefore, we used three juvenile *N. californicus* as IG-predators and expected increased egg predation in their presence. Second, an adult female *G. liturivorus* and three juvenile *N. californicus* were released onto leaf discs to test whether the presence of adult female *G. liturivorus* affects the survival of their eggs under threat of IG-predation. Third, we placed an adult female *G. liturivorus* alone on a leaf disc. Because an adult female *G. liturivorus* could continue oviposition during experiments, the third treatment served as a control for the effects of *G. liturivorus* on conspecific eggs.

Thrips larvae increase their feeding on eggs of the predatory mite *Iphiseius degenerans* on plants of low food quality (Janssen, Willemse, & Van Der Hammen, 2003). Consequently, to control Download English Version:

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