The influence of intraguild competitors on reproductive decisions by two predatory Heteroptera, Orius insidiosus (Anthocoridae) and Nabis americoferus (Nabidae)

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Available online: 20 Sep 2011

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RESEARCH ARTICLE

The influence of intraguild competitors on reproductive decisions by two predatory Heteroptera, *Orius insidiosus* (Anthocoridae) and *Nabis americoferus* (Nabidae)

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The relationship between the oviposition site preferences of predators in the face of intraguild competitors has received little attention, but it likely shapes the reproductive ecology of predatory species. In this study, oviposition intensity and the within-plant distribution of *Orius insidiosus* (Heteroptera: Anthocoridae) and *Nabis americoferus* (Heteroptera: Nabidae) eggs on *Phaseolus vulgaris* plants was studied when the two species were present independently or in combination. Both predators laid more eggs in the presence of the other species relative to when they were only exposed to conspecifics. When only exposed to conspecifics, *O. insidiosus* preferred to lay eggs on leaves and petioles on the upper half of the plant, whereas *N. americoferus* laid eggs mostly on the petioles and petiolules equally throughout the height of the plant. But when both species were present, *O. insidiosus* preferred to lay eggs on the leaf, whereas *N. americoferus* altered their behavior to lay an even greater proportion of their eggs on the petioles and petiolules. They altered their preferences for different plant strata too: *N. americoferus* laid more eggs on the upper quarter of the plant when *O. insidiosus* was present, and *O. insidiosus* was marginally more likely to lay eggs lower on the plant in the presence of *N. americoferus*. This study indicates that these two Cimicomorpha can detect the presence of one another, and that they adjust their reproductive decisions, presumably to avoid potential competitive interactions.

Keywords: predators; *Nabis americoferus*; *Orius insidiosus*; *Phaseolus vulgaris*; oviposition preference; predator–plant interactions

1. Introduction

Reproductive behavior of predatory arthropods influences the distribution and abundance of the predators within a habitat. Different factors influence the place where an egg is ultimately laid, ranging from the physiology of the mother and her egg, the biotic and abiotic characteristics of the environment, and the resource needs of the mother and her developing offspring (Seagraves 2009; Lundgren 2011). Their diverse reproductive behaviors and importance to biological control make predatory Heteroptera an excellent system to study how various constraints affect reproductive decisions.

In large part, the oviposition decision of predatory Heteroptera is affected by the relative survival and performance of the progeny. For predators that lay their eggs on

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plants, oviposition decisions are frequently influenced by plant characteristics and prey availability. Many cimicomorphan Heteroptera insert their eggs into plants at sites that promote offspring performance. For this reason, these species often have distinct preferences for different plants, and this is often manifested in increased offspring performance (Coll 1996; Sánchez, Gillespie, and McGregor 2004; Lundgren and Fergen 2006; Lundgren, Fergen, and Riedell 2008; Lundgren, Wyckhuys, and Desneux 2009). Within a plant species, these Heteroptera display additional preferences for specific plant tissues as oviposition substrates. Proposed mechanisms for these preferences include the thickness or resistance of the epidermis (Lundgren et al. 2008; Seagraves, Riedell, and Lundgren 2011), the relative densities of trichomes or leaf textures (Benedict, Leigh, and Hyer 1983; Richards and Schmidt 1996; Sigsgaard 2004; Lundgren et al. 2008), and the rate at which offspring are able to hatch from various structures (Groenteman, Guershon, and Coll 2006). Relative food availability (especially prey), may also affect the reproductive decision of a female. This is particularly well-studied in Anthocoridae. *Anthocoris nemorum* L., *Anthocoris nemoralis* Fabricius, and *Anthocoris confusus* (Reuter) all lay their eggs near high densities of prey (Evans 1976; Sisgaard 2004, 2005). More recently, Seagraves and Lundgren (2010) demonstrated that plant quality was most important in influencing the oviposition behavior of *O. insidiosus*, but when plant identity was constant, this predator laid more eggs on the plants with high prey abundance. In predatory Heteroptera, one source of potential prey that has been poorly explored within the context of reproductive ecology is the presence of competitors' eggs.

Another factor that may influence the final oviposition decision of a female predator is the presence of other natural enemies and their interactions, as is the case of the intraguild predation. The ladybird *Coleomegilla maculata* (DeGeer) prefers to oviposit on plants with glandular trichomes (Griffin and Yeargan 2002; Seagraves and Yeargan 2006) or in areas far from large aphids aggregations (Schellhorn and Andow 1999) to reduce predation on her eggs. Another predator that prefers to oviposit in sites with high trichome densities is the predatory midge *Aphidoletes aphidimyza* Rondani, whose females lay eggs in pubescent leaves where predation by coccinellids is reduced (Lucas and Brodeur 1999). Two hoverfly species, *Episyrphus balteatus* De Geer and *Metasyrphus corollae* Fabricius (Diptera: Syrphidae), responded differently to the presence of ladybird larvae: *E. balteatus* females oviposited less in the presence of the coccinellids, whereas *M. corollae* behavior was largely unaffected (Putra, Yasuda, and Sato 2009). Females of the predatory mite *Iphiseius degenerans* (Berl.) (Acari: Phytoseiidae) avoid predation on their eggs by ovipositing away from pollen resources, where their egg predators, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), forage for prey (Faraji, Janssen, and Sabelis 2001, 2002). There are some predators that even cease oviposition in the presence of other natural enemies: the predatory mite *Neoseiulus cucumeris* (Oudemans) is reluctant to oviposit in the presence of *I. degenerans* (Monserrat et al. 2007).

Orius insidiosus is an important native predator of crop pests in many agronomic systems in North America. This species is widely collected throughout much of North America east of the Rocky Mountains (Shapiro, Shirk, Kelley, Lewis, and Horton 2010), and is often a dominant foliar-dwelling predator in major field cropping systems such as corn (Isenhour and Marston 1981; Corey, Kambhampati, and Wilde 1998; Seagraves and Yeargan 2009), soybeans (Fox, Landis, Cardoso, and DiFonzo 2004; Rutledge, O'Neil, Fox, and Landis 2004), and alfalfa (Al-Deeb,

Wilde, and Zhu 2001). The damsel bug *Nabis americoferus* Carayon is also a common generalist predator in Midwestern field crops (Braman and Yeargan 1990) where it preys at least on leafminers (Guppy 1986) and Lepidoptera (Sloderbeck and Yeargan 1983). These two species of Heteroptera are sympatric in several crops, such as maize and beans (Coll and Bottrell 1995) or soybean (Isenhour and Yeargan 1982; Clements and Yeargan 1997). Within soybeans, *O. insidiosus* and *N. americoferus* prefer to reside on different plant parts, and are thus presumed to have minimal interactions (Clements and Yeargan 1997). A recent literature review on the reproductive ecology of predaceous Heteroptera by Lundgren (2011) discusses the possibility of an avoidance behavior between predators, but few studies directly compare how predatory Heteroptera adjust their oviposition behavior to avoid intraguild interactions.

The objective of this study was to evaluate the interactions among these two sympatric species. Specifically we addressed the hypotheses that in the presence of heterogeneric competitors, these bugs alter: (1) their oviposition intensity and (2) their placement of eggs on a plant, relative to when these predators are only exposed to conspecifics.

2. Material and methods

Green bean plants (*Phaseolus vulgaris* L.) were grown in the greenhouse from seed in a compost/peat-moss/perlite mixture and watered daily. Plants used in the experiment were between 19 and 27 days old and had between two and six internodes. The medium height plant per treatment was as follows: 15.83 ± 1.45 (*N. americoferus*), 14.48 ± 1.34 (*O. insidiosus*), and 15.58 ± 0.87 (both species together) with a total height per individual plant that varied from 5.3 to 25.9 cm.

Orius insidiosus and *N. americoferus* were field collected from alfalfa fields in Brookings, SD, USA. Field-collected adults were bred and maintained in climatic chambers ($25 \pm 1°C$, 70 ± 10 relative humidity (RH) and a 16 h L:8 h D photoperiod) for a maximum of two generations with *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs (Beneficial Insectary, Redding, CA, USA), water provided with a moistened cotton wick and green bean pods or green bean plants for *O. insidiosus* and *N. americoferus*, respectively. Offspring from field-collected *O. insidiosus* and *N. americoferus* were used in the experiments.

The experimental unit consisted of a single potted green bean plant enclosed within a cylindrical cage (39 cm tall and 12.5 cm diameter with 0.33-mm square mesh). The soil was covered with white sand to facilitate searching for the insects. Two pieces of a Post-it® (1 cm²; 3M St Paul, MN, USA), each with approximately 550–600 eggs of *E. kuehniella* affixed were added per plant. These two pieces were placed in the middle part of the plant, depending on its height. Also a few thrips were provided as a food source. These plants were randomly assigned to one of three treatments: (1) four *O. insidiosus* females ($n = 20$ plants), (2) four *N. americoferus* females ($n = 17$), and (3) two *O. insidiosus* females together with two *N. americoferus* females. For the latter treatment, plants were only included in the analysis for a given species if they laid eggs; this resulted in a sample size of 14 and 12 for *O. insidiosus* and *N. americoferus*, respectively. The experimental conditions were $25 \pm 1°C$, $70 \pm 10\%$ RH and a 16 h L:8 h D photoperiod and the insects were exposed to the

plants for 48 h. After that time the plants were kept refrigerated until the eggs laid by each insect could be counted microscopically. The number of eggs laid was classified according to five different plant structures: floret, leaf, internode, petiole and petiolule (Lundgren and Fergen 2006). Also, the length of each plant was divided into four segments, and the number of eggs laid by each species in each stratum was recorded (from lowest to highest, the strata were designated I–IV).

A one-way ANOVA was used to determine differences in the total number of eggs laid per female and treatment, means were separated with the Tukey test ($P < 0.05$). Those values were $\log + 1$ transformed to ensure the homoscedasticity of variances. Two-way ANOVAs were used to compare the effects of our treatments on oviposition patterns of these two bugs, with treatment and plant structure or plant stratum as main factors in the analysis. Means were separated with the LSD test. Separate analyses were conducted on *N. americoferus* and *O. insidiosus*. The one-way analyses were conducted using SAS Enterprise Guide 4.2 while the two-way analyses were conducted using SYSTAT 11.

3. Results

Nabis americoferus oviposition rate increased significantly and they preferred to lay eggs on different plant structures in the presence of *O. insidiosus* females than in the presence of conspecifics (treatment: $F_{1,135} = 9.52$, $P = 0.002$; plant structure: $F_{4,135} = 19.71$; $P < 0.001$; interaction: $F_{4,135} = 3.67$, $P = 0.007$). *Nabis americoferus* laid significantly more eggs on petioles than anywhere else on the plants (Figure 1A), and eggs were laid at similar rates on the remainder of the plant structures. Petioles ($F_{1,27} = 5.46$, $P = 0.03$) and petiolules ($F_{1,27} = 6.41$, $P = 0.02$) were the only structures where eggs were significantly more abundant in the treatment with both bugs compared with the *N. americoferus*-only treatment; eggs were laid at similar rates in the two treatments on florets, internodes, and leaves.

In contrast, oviposition rates and preferences of *O. insidiosus* females on the different plant structures were unaffected by the presence of *N. americoferus* (treatment: $F_{1,160} = 0.76$, $P = 0.38$; plant structure: $F_{4,160} = 13.23$; $P < 0.001$; interaction: $F_{4,160} = 1.23$, $P = 0.30$). However, even though differences were not significant ($F_{1,32} = 0.17$, $P = 0.69$), *O. insidiosus* laid a slightly higher mean number of eggs per plant per female in the presence of *N. americoferus* (Table 1). *Orius insidiosus* laid the most eggs on leaves and petioles, and the least number of eggs on the florets and internodes (Figure 1B).

The presence of *N. americoferus* did not affect the plant stratum where *O. insidiosus* preferred to lay eggs (treatment: $F_{1,128} = 0.55$, $P = 0.46$; plant stratum: $F_{3,128} = 12.23$, $P < 0.001$; interaction: $F_{3,128} = 2.17$, $P = 0.09$). Overall, most *O. insidiosus* eggs were laid higher on the plant (strata III and IV) in both treatments. *Orius insidiosus* laid marginally more eggs lower on the plant when *N. americoferus* was present, and higher on the plants (stratum IV) in the absence of *N. americoferus* (Table 1). Although *N. americoferus* laid significantly more eggs when *O. insidiosus* females were present, they laid their eggs equally throughout the height of the plant regardless of the presence or absence of *O. insidiosus* (treatment: $F_{1,108} = 5.91$, $P = 0.02$; plant stratum: $F_{3,108} = 1.23$; $P = 0.30$; interaction: $F_{3,108} = 0.58$, $P = 0.63$).
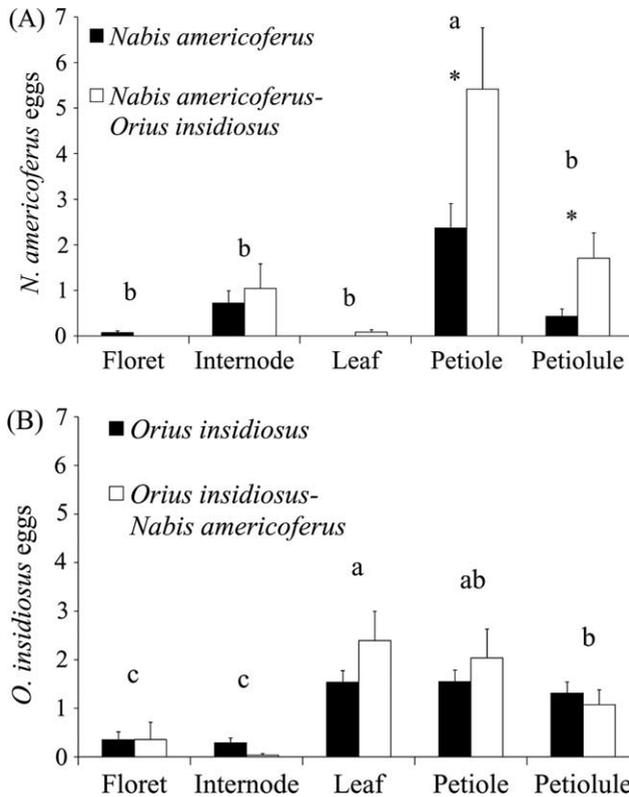
Figure 1. Mean (SEM) number of eggs laid per female per plant on different plant structures of *P. vulgaris* by *N. americoferus* (1A) and *O. insidiosus* (1B) alone and in the presence of their competitor.

Discussion

Orius insidiosus and *N. americoferus* are able to perceive the presence of interspecific competitors, and these predators adjust their oviposition patterns in response.

This research underscores that predators often prefer to lay eggs in certain strata throughout the height of a plant, and that the presence of interspecific competitors can alter these preferences (Table 1). In the absence of *N. americoferus*, *O. insidiosus* laid marginally more eggs in the upper strata (stratum IV) of the bean plants. In the presence of *N. americoferus*, *O. insidiosus* laid marginally more eggs in lower strata (strata II and III). Moreover, although it was not statistically significant, *N. americoferus* appeared to lay a greater proportion of eggs in lower strata (strata II and III) when *O. insidiosus* was absent; when *O. insidiosus* was present, *N. americoferus* laid three times more eggs higher on the plant (stratum IV). The literature reveals that predatory heteropterans display oviposition preferences for areas along the height of a plant, but the literature suggests that these preferences are neither consistent among or with species. van den Meiracker and Sabelis (1993) demonstrated that *O. insidiosus* prefers to oviposit in the growing tips of caged sweet pepper plants. Another study carried out by Graham and Jackson (1981) showed that *Orius*

Table 1. Mean (SEM) number of eggs laid per female per plant on *P. vulgaris* by *N. americoferus* and *O. insidiosus* when the bugs were caged alone and with the competitor.

| | *N. americoferus* | | *O. insidiosus* | |
Stratum	Alone	With *O. insidiosus*	Alone	With *N. americoferus*
I	0.46 ± 0.21	1.00 ± 1.00	0.04 ± 0.02[b]	0.04 ± 0.03[b]
II	1.16 ± 0.31	1.92 ± 1.13	0.71 ± 0.33[b]	1.61 ± 0.58[a]
III	1.12 ± 0.31	2.21 ± 0.81	1.89 ± 0.40[a]	2.75 ± 0.49[a]
IV	0.85 ± 0.29	3.00 ± 1.20*	2.40 ± 0.60[a]	1.50 ± 0.36[a]
Total eggs/plant/female	3.59 ± 0.59	8.25 ± 1.71*	5.04 ± 0.51	5.89 ± 0.92

Sample sizes were 12 and 14 plants for *N. americoferus* and *O. insidiosus*, respectively. Strata are numbered lowest to highest; differences among strata (within a column) are indicated by lower case letters (columns without letters were not significant); asterisks indicate significant differences ($\alpha = 0.05$) between columns within a species (differences between treatments within a stratum).

tristicolor (White) (Heteroptera: Anthocoridae) preferred to oviposit in the upper and longer stems of alfalfa plants. To the contrary *O. insidiosus* did not show clear preferences for ovipositing in specific nodes along the stem of green bean plants in a study carried out by Lundgren and Fergen (2006). The results obtained for *N. americoferus* in previous experiments depend on the plant species used. More eggs were found in the upper parts of alfalfa (Richards and Harper 1978; Graham and Jackson 1982) and soybean stems (Braman and Yeargan 1989). Pfannenstiel and Yeargan (1998) found that eggs distribution appears to be dependent on plant morphological characteristics: *Nabis roseipennis* Reuter (Heteroptera: Nabidae) laid more eggs in the lower third of corn, tomato and tobacco but this same species laid more eggs in the middle and upper parts of squash and soybean. In a field experiment where *O. insidiosus* and *N. roseipennis* were presented together on soybean, *O. insidiosus* preferred to oviposit on the top portions of the plant and *N. roseipennis* restricted its oviposition to the mid-section of the plants (Isenhour and Yeargan 1982). Our results are consistent with the hypothesis that, in the other's presence, *O. insidiosus* descends to lower levels and *N. americoferus* ascends to higher levels within a plant. It is also important to acknowledge that certain plant structures are found disproportionately across plant strata (for example, often more petioles are found higher on the plants), and thus the location of preferred plant structures could account for which plant strata are preferred.

In addition to plant stratum, the two predators studied showed distinct oviposition preferences for different plant structures in green bean plants (Figure 1). *Orius insidiosus* preferred to oviposit in the leaves and petioles, while *N. americoferus* preferred to oviposit in the petioles. Although they displayed preferences for different structures, avoidance was not complete; both species oviposited in petioles and petiolules. Moreover in the presence of *O. insidiosus*, *N. americoferus* laid significantly more eggs in the petioles and petiolules than in its absence. Seagraves et al. (2011) found that *O. insidiosus* preferred to oviposit in the leaves of green bean plants, but oviposition shifted to the petioles when these plants were water stressed. In contrast, Lundgren and Fergen (2006) found that most of the

eggs laid by *O. insidiosus* in green bean plants were laid in the petiolules and petioles, and less in the leaves. Another anthocorid, *A. confusus*, laid the majority of its eggs in the leaves of broad bean plants in a long-term laboratory study, but this depended on the prey distribution on the leaves (Evans 1976). In apple and pear leaves, *A. nemorum* preferred to lay their eggs near leaf margins on the ventral side of damaged leaves, whereas *A. nemoralis* laid their eggs on the leaf vein on the dorsal side of healthy leaves (Sisgaard 2004). In a laboratory experiment, Pfannenstiel and Yeargan (1998) found that *N. roseipennis* laid significantly more eggs in the petioles of soybean and squash plants than in any other plant structure. When eggs of both species were sampled at the same time in a soybean field, more *O. insidiosus* and *N. americoferus* eggs were found in the petioles while more *N. roseipennis* eggs were found in the petiolules (Isenhour and Yeargan 1982). Clearly, the oviposition preferences for specific tissues by predatory heteropterans are quite plastic, influenced by the bug and plant species involved, and the current biotic (especially local resource availability) and abiotic conditions.

Finally, we hypothesize that avoidance of predation or competition is partially responsible for the shift in oviposition behavior by these predatory bugs. Some studies have observed predation on *O. insidiosus* in the field by other predator taxa: *N. americoferus* attacks *O. insidiosus* adults and nymphs in soybean fields (Braman and Yeargan 1989), and *Geocoris* spp. attack *Orius* spp. in cotton fields (Loya-Ramírez, García Hernández, Ellington, and Thompson 2003; Rosenheim 2005). Thus, we suspect that eggs are at risk of predation by other predatory bugs, which may explain why eggs are inserted into plant tissue in the first place (Lundgren 2011). Another observation we made was that *N. americoferus* increased oviposition 2.3-fold when *O. insidiosus* was present. There may be different explanations for this behavior. It is possible that preferred oviposition sites are limiting on a given plant, and reducing the number of conspecifics from four to two allowed the remaining females to exploit these preferred sites more completely. Groenteman et al. (2006) found that mated *O. albidipennis* females defended preferred oviposition sites along the veins of cotton leaves against other females. If *N. americoferus* perceives *O. insidiosus* as prey, the former may increase its oviositon rate to fully exploit this food source. Finally, plants defend themselves from traumatic oviposition by predatory Heteroptera (De Puysseleyr, Höfte, and De Clercq 2011), and the alterations in the plant's physiology could affect subsequent oviposition behavior of predatory bugs. Differences in oviposition intensity when interspecific competitors were present or absent was greater for *N. americoferus* than for *O. insidiosus*. It is possible that these two bugs affect this immune response of the plant differently and that this might explain this pattern. We conclude that oviposition preferences of important predators are influenced by intraguild interactions and to fully understand the mechanisms involved in this behavior, as well as its implications under more realistic conditions, additional future work is warranted.

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