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Oviposition response by *Orius insidiosus* (Hemiptera: Anthocoridae) to plant quality and prey availability

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ABSTRACT

The predator *Orius insidiosus* consumes a mixed diet of prey, vascular sap, and plant-based foods through its life. Plant species identity affects the oviposition behavior of *O. insidiosus* in that it prefers plants where newly hatched nymphs perform best, in the absence of prey. Choice tests were conducted in the laboratory to determine if the presence of a high-quality prey item (Lepidopteran eggs) affects oviposition choice in a monoculture and also how prey presence affects oviposition preference for plants of high (i.e., green bean, *Phaseolus vulgaris*) or low (soybean, *Glycines max*) suitability for *O. insidiosus*. *O. insidiosus* laid 56.4% more eggs on prey-free *P. vulgaris* than prey-free *G. max*. The presence of prey on *P. vulgaris* increased oviposition on those plants by 26.4% over that laid on prey-free *P. vulgaris*. When *G. max* with prey was presented alongside prey-free *P. vulgaris*, *O. insidiosus* still laid 55.4% more eggs on the latter. Prey availability affects oviposition on plants of equivalent quality, but plant suitability over-rides the importance of prey availability for this zoophytophagous insect. Phytophagy in young nymphs is important for their survival and we hypothesize that *O. insidiosus* females are better able to forecast plant quality than future prey populations as resources for their offspring.

1. Introduction

In order to maximize their reproductive success, insects use a variety of cues to determine the quality of a potential oviposition site. In herbivorous insects, reproductive females weigh the suitability of plant-based resources for their developing offspring, and often oviposit on plants and plant parts where they will perform best (Jaenike, 1978; Craig et al., 1989; Stein and Price, 1995; Craig and Ohgushi, 2002; Scheirs et al., 2003). Carnivorous insects also evaluate prey quality and availability when making oviposition decisions. One example is the evaluation of hosts prior to oviposition by hymenopteran parasitoids (Vinson, 1998), but predators also lay eggs in response to prey abundance and quality (Seagraves, 2009). Many important biological control agents are true omnivores, in that they feed at more than one trophic level (Coll and Guershon, 2002; Lundgren, 2009). It is currently unknown how omnivores balance their offspring's need for plant and prey resources when making egg laying decisions.

Orius insidiosus Say (Heteroptera: Anthocoridae) is recognized as a predator on many economically important pests in various cropping systems (Reid, 1991; Rutledge et al., 2004; Sansone and Smith, 2001; Baez et al., 2004; Seagraves and Yeargan, 2009). In addition to prey *O. insidiosus* feeds on plant vascular sap and pollen (Kiman and Yeargan, 1985; Naranjo and Gibson, 1996; Armer et al., 1998; Corey et al., 1998). In some instances *O. insidiosus* and other predatory bugs can develop to the next instar or even complete development on a plant-only diet (Kiman and Yeargan, 1985; Naranjo and Gibson, 1996; Coll, 1998; Lundgren, 2009). The addition of prey into the diet often benefits immature development time and survival, as well as adult longevity and fecundity (Cocuzza et al., 1997; Coll, 1998).

O. insidiosus inserts its eggs into plant tissue, and under artificial conditions other substrates, such that only the operculum is exposed (Isenhour and Yeargan, 1982; Lundgren and Fergen, 2006). Eggs are not laid randomly; the mother uses physical cues such as trichome density, epidermal thickness, turgor, and substrate shape to inform placement (Shapiro and Ferkovich, 2006; Lundgren et al., 2008; Seagraves et al., submitted for publication). This leads to directed preferences for specific plant tissues (Isenhour and Yeargan, 1982; Groenteman et al., 2006; Lundgren et al., 2008) and ultimately manifests itself in distinct preferences for certain plant species (Coll, 1996; Lundgren and Fergen, 2006). The preference for plant species correlates with the lifespan of nymphs on those plants in the absence of prey (Lundgren et al., 2008). Given that plant species and prey availability affect nymphal survival, our goal was to examine how reproductive decisions of female *O. insidiosus* are made when these two nutritional variables (plant quality and prey availability) are manipulated. Specifically, we examined oviposition preferences of *O. insidiosus* for (1) green bean (*Phaseolus vulgaris*; a preferred plant) and soybean (*Gly-*

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cines max; a less preferred plant) plants in the absence of prey, (2) green bean plants with and without *Ephestia kuehniella* Zeller (Lepidoptera: Phycitidae) eggs (a high-quality prey item), and (3) green bean plants without prey and soybean plants with prey.

2. Methods

Plastic pots (3.8 cm diameter by 21 cm height; Model SC-10; Stuewe & Son Inc., Tangent OR) were filled to 18.5 cm height with a compost/peat-moss/perlite potting media (MiracleGro Inc., Marysville, OH) containing a slow-release fertilizer (NPK: 0.21–0.07–0.14). Two green bean (cv 'Jade') or soybean (var. 'Pioneer 91B91') seeds were placed in each pot. Pots were then filled to capacity with potting mix, watered to saturation and then once every 2 d, covered with aluminum foil, and placed into a growth chamber (Model 3245; Conviron Inc., Winnipeg, Canada) at constant 20 °C temperature and 50% relative humidity (rh). High pressure sodium and metal halide lamps in a 20:80 mixture were set to provide a 14:10 L:D photophase at 550 µmol s^{-1} m^{-2} of photosynthetically active radiation. Foil covers were removed 6 d after planting. Seedlings, which began to emerge from the soil after 4–5 d, were thinned to one plant pot^{-1} about 8 d after planting. Plants used in oviposition preference tests were between 19 and 24 d after planting and had the first trifoliate fully expanded.

O. insidiosus were field-collected, mainly from alfalfa, in Brookings Co., SD. These bugs were brought indoors and provided a moistened cotton wick, previously frozen *E. kuehniella* Zeller eggs (Beneficial Insectary, Redding, CA), and green beans. Offspring from the field-collected individuals were used in the oviposition preference tests. *O. insidiosus* (six females and two males; between 2 and 5 d old) were placed in cages (43 cm tall and 23 cm diameter with 0.33 mm square mesh) in which two whole potted plants were presented. A saturated cotton wick was included in each cage. Experimental conditions were 25 °C, 50% rh, and 14:10 (L:D) and *O. insidiosus* were exposed to plants for 48 h.

Three oviposition preference tests were conducted. The first trial was a choice test between green bean and soybean ($n = 14$ replicates), where prey was not associated with either plant species. In this experiment, *E. kuehniella* eggs were provided as food in a small weigh boat on the base of the cage, equidistant to both plants. The next trial involved a choice test between randomly assigned green bean with and without *E. kuehniella* eggs ($n = 20$). In this trial, 50 previously frozen prey eggs per plant were attached individually to the adaxial surface of leaves with a fine camel hair paintbrush and a 5% solution of gum arabic (Product # G9752, Sigma–Aldrich, St. Louis, MO, United States) (modified from Chen and Feng, 2006). This prey density in pre-testing resulted in some eggs not being consumed, thus food would be available throughout the trial. The final trial used a similar approach to assess the preference of *O. insidiosus* for prey-free green bean and soybean with *E. kuehniella* eggs ($n = 20$). After 48 h, the remaining females per cage were recorded, and plants were examined under a microscope to determine the number of *O. insidiosus* eggs laid. Square-root transformed mean numbers of *O. insidiosus* eggs were compared between treatments using a paired *t*-test. Additionally, the numbers of *E. kuehniella* eggs attacked, missing, or still intact were recorded, and proportions of eggs meeting each fate were compared between prey-enriched green bean and prey-enriched soybean using a Kruskal–Wallis test. Eggs that were shriveled, tepee-shaped, and devoid of contents were considered attacked (Fletcher and Thomas,1943).

3. Results

O. insidiosus laid more eggs on prey-free green bean than prey-free soybean ($t = 5.91$, $P < 0.01$, $df = 13$) (Fig. 1A). Significantly more *O. insidiosus* eggs were laid on green bean with prey than on prey-free green bean ($t = 3.22$, $P < 0.01$, $df = 19$) (Fig. 1B). A greater number of eggs were laid on green bean without prey, even when *G. max* were enriched with prey ($t = 5.58$, $P < 0.01$, $df = 19$) (Fig. 1C).

E. kuehniella eggs were attacked more often when placed on green bean compared to soybean ($H = 25.92$, $P < 0.01$, $df = 1$) (Table 1). More eggs were intact or missing when placed on soybean compared to those placed on green bean (intact: $H = 17.64$, $P < 0.01$, $df = 1$; missing: $H = 4.41$, $P = 0.03$, $df = 1$) (Table 1).

4. Discussion

Plant species plays a more prominent role in oviposition site selection for *O. insidiosus* than prey availability. When given a choice involving a single plant species, *O. insidiosus* laid more eggs on prey-enriched plants than on prey-free plants. However, when presented with different plant species, plant identity over-rides prey availability in the decision-making process of reproductive *O. insidiosus*. We hypothesize that plant suitability for newly hatched offspring is important and easier to forecast than future prey populations, and is a primary factor in the selection of oviposition sites for this zoophytophagous predator.

When presented with plants of different species, *O. insidiosus* displayed specific preferences for certain species. In this case, the bug laid more eggs on green bean than on soybean. This is specifically in accord with results previously reported by Lundgren and Fergen (2006) and generally with reports of preference among plant species (Coll, 1996). This oviposition preference remains largely unchanged even when the plant of lesser preference was enriched with prey items. Whereas in a comparison within a single plant species, prey enrichment had a strong positive effect on oviposition. Among holometabolous herbivores and parasitoids, larval food or site of adult eclosion sometimes influences adult oviposition behavior (Messing and Rabasse, 1995; Akhtar and Isman, 2003). Even in these examples, innate preferences are more important in determining oviposition preference (Messing and Rabasse, 1995; Barron, 2001; Janz et al., 2009). We are not aware of any evidence that prior exposure of *O. insidiosus* females in our experiments to mature green bean pods would have influenced our results (e.g., vegetative green bean being preferred to soybean). Additionally, *O. insidiosus* displays oviposition preferences for plant species that they have had no prior experience with under field and

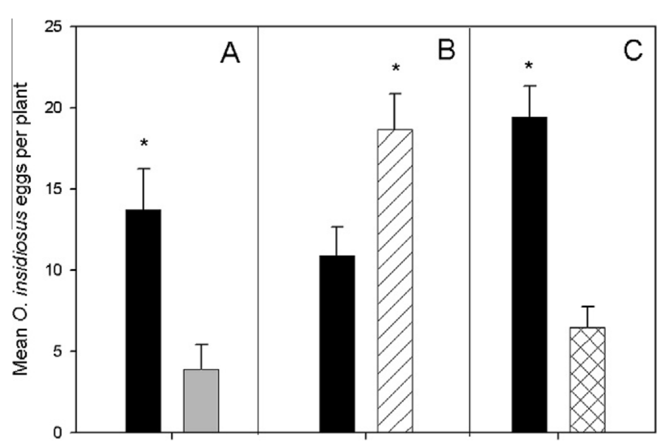

Fig. 1. Effect of prey enrichment and plant species on *Orius insidiosus* oviposition. (A) Oviposition choice between prey-free green bean (black bar) and prey-free soybean (gray bar) ($N = 14$). (B) Oviposition choice between prey-free green bean (black bar) and prey-enriched green bean (diagonal hatch) ($N = 20$). (C) Oviposition choice between prey-free green bean (black bar)and prey-enriched soybean (crosshatch) ($N = 20$).Values represent mean + SEM. * Signifies that means are significantly different (paired *t*-test, $\alpha = 0.05$).

Table 1
Percentage of *Ephestia* sp. eggs that were intact, attacked, or missing when placed on green bean or soybean and exposed to *Orius insidiosus* for 48 h.

	Intact	Attacked	Missing
Green bean	20.00 ± 2.11a	59.10 ± 3.05a	20.90 ± 2.62a
Soybean	50.50 ± 4.69b	18.90 ± 2.80b	30.60 ± 3.67b

Fifty eggs were placed on the adaxial surface of leaves using a fine camel hair brush and a 5% solution of gum arabic as an adhesive. Column means followed by the same letter are not significantly different (Kruskal–Wallis, $\alpha = 0.05$).

laboratory conditions, suggesting that their oviposition behavior is driven by innate preferences for plants with particular physical and nutritional characteristics (Lundgren and Fergen, 2006; Lundgren et al., 2008, 2009).

In a comparison between plants of a single species, prey enrichment shifted oviposition toward the plant enriched with prey. Several studies have speculated or indirectly examined the effect of prey presence and abundance on oviposition by predaceous Heteroptera. Isenhour and Yeargan (1982) speculated that *O. insidiosus* oviposition frequently occurs where soybean thrips are most abundant and *Nabis roseipennis* eggs occurred where green cloverworm eggs abound. However, Pfannenstiel and Yeargan (1998) demonstrated that *N. roseipennis* made choices among plant species independent of prey distribution. *Geocoris punctipes* prefers particular weed species for oviposition but this preference is not influenced by prey abundance (Naranjo and Stimac, 1987). *Orius laevigatus* oviposited more frequently on plants with a preferred prey than a lesser quality prey (Venzon et al., 2002). Our results demonstrate that prey abundance affects the amount of oviposition by *O. insidiosus* on a plant when plant species identity is constant.

More prey were consumed on green bean than soybean. *O. insidiosus* has different foraging strategies and efficiencies among different plant species (Coll et al., 1997). It is possible that the time spent on green bean contributed to the observed higher frequency of oviposition on this plant. However, prey was still consumed on soybean, although few eggs were laid on this plant; this suggests that *O. insidiosus* is foraging on soybean, but is making an active choice to oviposit on green bean, even if there is no prey available on this plant.

There is a growing body of literature that suggests that *O. insidiosus* oviposition decisions are driven by the physical and physiological characteristics of plants (Coll, 1996; Groenteman et al., 2006; Lundgren and Fergen, 2006; Lundgren et al., 2008; Seagraves et al., accepted for publication). Preference for particular plant species is correlated with the performance of newly hatched nymphs on these plants in the absence of prey (Lundgren et al., 2008, but see Coll, 1996). The results of our study demonstrate the relative importance of plant-based factors over prey in the reproductive decisions of an omnivorous predator and suggest that plant nutritional quality for newly hatched nymphs is an important consideration. Additionally, plant quality is likely to be more reliably determined relative to the challenge of forecasting prey populations at the time of egg hatch. Information on how this important natural enemy makes its reproductive decisions will give insight into the importance of plant feeding and inform what resources are needed to design cropping systems with increased biological control (Shaltiel and Coll, 2004; Lundgren, 2009; Lundgren et al., 2009).

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