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Oviposition habitat influences egg predation of native and exotic coccinellids by generalist predators

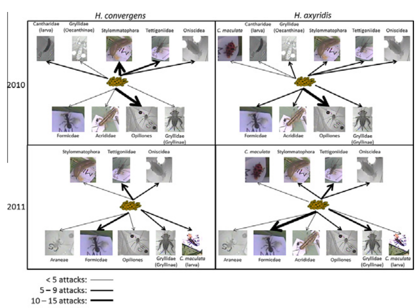
Chelsea A. Smith *, Mary M. Gardiner

Department of Entomology, The Ohio State University, Ohio Agricultural Research & Development Center, Wooster, OH 44691, USA

HIGHLIGHTS

- A diverse guild of generalist predators attack coccinellid egg masses.
- Exotic coccinellids are not important predators of coccinellid egg masses.
- Egg predation rate and predator guild vary among species and oviposition habitats.

GRAPHICAL ABSTRACT



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ABSTRACT

Native coccinellid decline has been documented worldwide. An elevated level of predation on native coccinellid eggs versus exotic coccinellid eggs has been proposed as a mechanism that may favor the reproductive success of exotic species. Recently, we determined that the native coccinellid *Hippodamia convergens* incurs significantly greater egg predation than the exotic *Harmonia axyridis*. The goal of this study was to determine if oviposition habitat or the presence of alternative prey affected the composition or contribution of egg predator guilds attacking native and exotic coccinellid eggs. Within alfalfa, grassland, and soybean habitats we identified the predator guild consuming *H. convergens* and *H. axyridis* eggs using video surveillance. We quantified the contribution of each predator to egg predation, and determined whether the abundance of aphids altered predation intensity. Our findings did not indicate that exotic coccinellids were significant predators of coccinellid eggs. However, the predator guild detected was diverse and varied across habitats. The greatest diversity and highest levels of egg predation were found within grasslands but we did not detect significant differences in the guild of predators attacking the two egg species. Thus, greater predation of *H. convergens* egg masses resulted from a higher proportion of eggs consumed by a shared guild, and not due to a more diverse predator pool. The majority of predators were just as likely to attack either egg species; however, we did find that in both 2010 and 2011, Formicidae maintained a consistent predation preference for *H. axyridis*. We found no correlation between the relative abundance of aphids and prevalence of coccinellid egg predation and herein, we discuss the implications of these findings for native coccinellid conservation and biological control.

1. Introduction

Several multi-year censuses have illustrated population declines among native North American lady beetle species (Coleoptera: Coccinellidae) coinciding with the establishment of exotic lady beetles (Alyokhin and Sewell, 2004; Colunga-Garcia and Gage, 1998; Elliott et al., 1996; Evans, 2004; Gardiner et al., 2009;

* Corresponding author. Address: Department of Entomology, The Ohio State University, Ohio Agricultural Research & Development Center, 1680 Madison Ave., Thorne Hall, Wooster, OH 44691, USA. Fax: +1 330 263 3686.

E-mail addresses: smith.7231@osu.edu (C.A. Smith), gardiner.29@osu.edu (M.M. Gardiner).

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Turnock et al., 2003; Wheeler and Hoebeke, 1995). Although many factors may have contributed to native coccinellid decline, several studies implicate exotic competitors as the primary cause. For example, Wheeler and Hoebeke (1995) attributed the decline of the once common nine spotted lady beetle, *Coccinella novemnotata* (Herbst), to an increase of the exotic *Coccinella septempunctata* (L.) in the Northeastern United States and less than 100 *C. novemnotata* individuals have been documented in North America since 2008 (Losey et al., 2012). A 20-fold reduction in populations of *Coccinella transversoguttata* (Faldermann) and *Adalia bipunctata* (L.) was observed in South Dakota by Elliott et al. (1996), who attributed the declines to the establishment of *C. septempunctata* in the region. Similarly, Colunga-Garcia and Gage (1998) reported a decrease in *Brachiacantha ursina* (Fabricius), *Cycloneda munda* (Say), and *Chilocorus stigma* (Say) abundance following the establishment of *Harmonia axyridis* (Pallas) in Michigan. Furthermore, Gardiner et al. (2009) failed to detect the previously-abundant *Hippodamia convergens* (Guérin-Méneville) within the states of Michigan and Ohio and demonstrated that landscape may affect the distribution of native and exotic coccinellids, hypothesizing that native coccinellids may only thrive in landscapes less favorable to exotic species.

To date, the majority of research examining the role of exotic coccinellids in native coccinellid decline has focused on interference competition via the intraguild predation (IGP) hypothesis, proposing that observed population declines among native lady beetles are the result of IGP by exotic coccinellids. This hypothesis is supported by several studies conducted in the laboratory, which have illustrated that exotic lady beetles, primarily *H. axyridis* and *C. septempunctata*, have a propensity to act as intraguild predators of native lady beetle eggs and larvae (Cottrell, 2004, 2005, 2007; Snyder et al., 2004; Sato et al., 2005). Additionally, *H. axyridis* has been observed feeding on *C. maculata* egg masses in sweet corn, however, these events were rare (Cottrell and Yeargan, 1998a,b). Further support of the IGP hypothesis is demonstrated from an analysis of *H. axyridis* larvae from Belgian lime trees revealing traces of alkaloids from native species, suggesting that exotic larvae are consuming native coccinellids (Hautier et al., 2011). In addition, DNA of native coccinellids was also detected within exotics collected from soybean fields in Québec (Gagnon et al., 2011).

Although exotic coccinellids are known to act as intraguild predators in the laboratory and field, studies documenting the significance of these IGP interactions on native lady beetle decline have yielded varied results. Hoogendoorn and Heimpel (2004) observed that the presence of *H. axyridis* larvae did not impact the survival or weight gain of native *Coleomegilla maculata* (De Geer) larvae in field cages, suggesting that *H. axyridis* may not have a negative effect on this species. Conversely, Gardiner et al. (2011) found that *C. maculata*, did experience significant egg predation within soybean fields, although the contribution of exotic lady beetles to that predation was not measured and the abundance of exotic coccinellids was not a strong predictor of coccinellid egg predation. Thus, exotic coccinellids may be contributing to predation on native coccinellid egg masses, although this may not be driving the decline of native species.

Recently, Smith and Gardiner (in press) found that *H. convergens* sustains significant egg loss in croplands and grasslands, with up to 88% of eggs removed by predators within 48 h of exposure. *H. convergens* frequently experienced significantly greater egg predation than *H. axyridis*; up to a 33% difference in egg removal was found between these species and it was predicted that exotic coccinellids were responsible for the detected egg predation. However, preliminary video surveillance illustrated that a diversity of arthropods, including Stylommatophora, Opiliones, Oniscidea, *C. maculata*, Gryllidae, Cantharidae, Tettigoniidae, Acrididae, and Formicidae feed upon lady beetle eggs in the field. The goals of this study were to quantify and compare the guild of predators attacking native and exotic coccinellid eggs in crop and semi-natural habitats, and to determine if extraguild prey influenced the risk of attack. To address these goals we completed three objectives: (1) determine how predator guild diversity and abundance varies across coccinellid foraging habitats; (2) examine if the abundance of aphid prey present within a habitat influenced the magnitude of coccinellid egg predation, and (3) measure whether egg predators are associated with *H. convergens* or *H. axyridis* eggs. We predicted that: (1) the egg predator guild will be more diverse in semi-natural grassland habitats compared to cropland; (2) eggs within habitats harboring high aphid populations will be subjected to less predation compared with habitats where aphids are rare; and (3) a greater number of predator taxa will be associated with predation on native coccinellid eggs than on exotic egg masses.

2. Materials and methods

2.1. Study sites

Alfalfa, grassland, and soybean sites were identified within eight counties throughout Ohio (one site of each habitat within Delaware, Fayette, Huron, Knox, Perry, Putnam, Shelby, and Wayne Co.) (Fig. 1). In 2010, data were collected from six grasslands, four alfalfa, and four soybean fields between June 18 and August 13. Each site was visited once with the exception of the alfalfa site in Wayne Co. and grassland site in Huron Co., which were visited twice, and the grassland site in Wayne Co., which was visited three times (Table 1). In 2011, data were collected within all sites between June 14 and July 26. All sites were visited once, except for three alfalfa sites (Knox, Perry, and Wayne counties), and all eight of the grassland sites where data was collected twice (Table 1). Grower-collaborators managed the soybean and alfalfa sites. Growers did not alter management practices during this study, and it is likely that some alfalfa fields were sprayed for alfalfa weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae), early in the season. However it is unlikely that fields were sprayed for soybean aphid, *Aphis glycines* (Matsumura) (Hemiptera: Aphididae), due to populations remaining well below the economic threshold

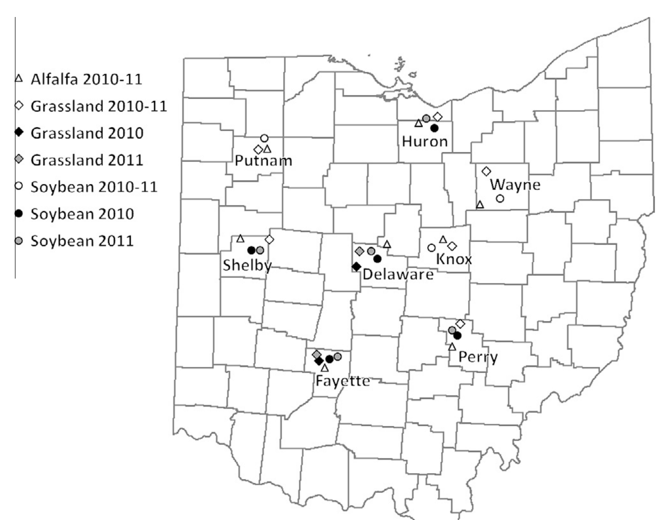

Fig. 1. Map of field sites. Map of Ohio depicting the network of alfalfa, grassland, and soybean fields where experiments and sampling were conducted. The same fields were used in 2010 and 2011, except for grassland in Delaware, and Fayette counties (the 2010 grasslands were determined to be unsatisfactory for the use of video cameras), and soybean sites in Huron, Shelby, Delaware, Fayette, and Perry counties (due to crop rotation).