



Complementary effects of resident natural enemies on the suppression of the introduced moth *Epiphyas postvittana*

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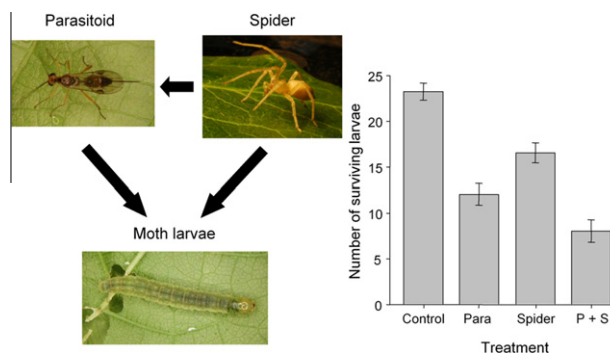
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HIGHLIGHTS

- ▶ The effects of parasitoids and spiders on an introduced moth were assessed.
- ▶ The spider appeared to reduce numbers of adult parasitoids.
- ▶ Both the parasitoid and the spider increased larval mortality of the moth.
- ▶ Interactive effects of the parasitoid and spider were additive.

GRAPHICAL ABSTRACT

The combined effects of parasitoids and spiders on moth larvae were additive and did not differ from the sum of their individual impacts, despite possible spider predation on parasitoids.



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ABSTRACT

Generalist predators may disrupt or complement biological control by parasitoids. Past studies have examined how predators and parasitoids interact to affect aphid suppression, but more information is needed from other host taxa. Here, we explore the interactive effects of a spider (*Cheiracanthium mildei*) and a generalist parasitoid (*Meteorus ictericus*) on the light brown apple moth (*Epiphyas postvittana*), a recent introduction to North America. The spider negatively affected adult parasitoids in a field experiment, and reduced numbers of parasitized larvae in the laboratory. Nonetheless, the combined effects of parasitoids and spiders on larval mortality of the moth were additive. Percent parasitism was not affected by the presence of the spider in field or laboratory experiments, and results were similar when single or multiple larval instars of the moth were included. The spider's lack of prey preference for unparasitized or parasitized larvae likely precluded any disruptive effects on parasitism. Results suggest that resident generalist parasitoids and predators can work in conjunction to hinder the invasion success of a novel herbivore prey species.

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1. Introduction

Research attention has increasingly focused on the consequences of biodiversity losses for biological control (Straub et al.,

2008). Higher diversity within natural enemy communities can enhance herbivore suppression and strengthen positive effects on plants (Snyder et al., 2006). Generalist predators can prey on other natural enemies, however, thus compromising effects on herbivores and dampening trophic cascades (Polis and Holt, 1992; Finke and Denno, 2004). An intraguild predator is likely to disrupt herbivore suppression if it is an inefficient consumer of herbivores, or if it selectively preys on other predators (Rosenheim et al., 1993). On the other hand, an intraguild predator that efficiently consumes

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herbivores can strengthen biological control, despite its effects on other natural enemies (Colfer and Rosenheim, 2001; Hogg and Daane, 2011).

Research has often focused on either predator–prey or parasitoid–host interactions, although most communities are likely to include both predators and parasitoids (Mommott et al., 2000). Interactions between parasitoids and predators are typically unidirectional, with predators preying on parasitoids (Brodeur and Rosenheim, 2000). Predators can consume adult parasitoids or immature parasitoids within parasitized hosts (Meyhöfer and Hindayana, 2000; Colfer and Rosenheim, 2001); endoparasitoids may be especially vulnerable to intraguild predators (Bilu and Coll, 2007). Predation can hinder parasitism rates (Snyder and Ives, 2001; Costamagna et al., 2007), particularly if parasitoids cause more herbivore mortality than predators (Rosenheim, 1998). Indeed, the failure of many introduced parasitoids to regulate host populations may be due to predation (Brodeur and Rosenheim, 2000). The effects of predators and parasitoids in combination can also be complementary, however (Schmidt et al., 2003; Snyder and Ives, 2003; Bilu and Coll, 2007). The outcomes of predator–parasitoid interactions are likely to hinge on the relative impacts of predators on unparasitized and parasitized hosts. Predators may attack parasitized hosts in proportion to their availability, or they may show a partial or absolute preference for unparasitized or parasitized prey (Rosenheim, 1998). Parasitism may alter host behavior in ways that increase vulnerability to predation (Snyder and Ives, 2001).

Past studies have explored the interactive effects of parasitoids and predators on aphid suppression (e.g., Snyder and Ives, 2003), but there is little or no information from other systems. This study focuses on the role of parasitoid–predator interactions in the suppression of the light brown apple moth (LBAM) *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), a native of Australia that has recently invaded California. LBAM poses a threat to North American crops and ornamental plants due to its exceptionally wide host range (Suckling and Brockerhoff, 2010). LBAM has yet to reach outbreak status in California, however, and its population or range expansion may be limited by climatic tolerances (Gutierrez et al., 2010) and resident natural enemies (Wang et al., 2012). Parasitism of LBAM has been reported throughout its range (Suckling and Brockerhoff, 2010), and generalist predators, particularly spiders, have been implicated in the high mortality rates of LBAM larvae in Australia (Danthanarayanan, 1983).

We examined the effects of a generalist predator, the spider *Cheiracanthium mildei* L. Koch (Miturgidae), and a parthenogenetic larval–endoparasitoid, *Meteorus ictericus* Nees (Hymenoptera: Braconidae) on the density of LBAM larvae feeding in French broom (*Genista monspessulana* (L.) L. Johnson), which is commonly infested by LBAM in the San Francisco Bay Area of California. According to a recent field survey in this region, *M. ictericus* accounted for >80% of the total larval parasitoids associated with LBAM, and was collected from 39 of the 70 sampled LBAM-infested plant species, including French broom (Wang et al., 2012). LBAM larvae parasitized by *M. ictericus* show reduced growth relative to unparasitized larvae, and die shortly after the larval parasitoid has exited for pupation (X.G. Wang, unpubl.). *C. mildei* is a wandering spider that actively searches for prey and does not build a web. It occurs throughout California and is abundant in French broom and a variety of other LBAM host plants (B.N. Hogg, unpubl.). French broom, *M. ictericus* and *C. mildei* are all non-native to California, providing an opportunity to assess the effects of an entirely exotic food web on the subsequent invasion of a novel herbivore species. Using a combination of field and laboratory experiments, we assessed whether: (1) spiders disrupt or complement suppression of LBAM larvae by parasitoids; (2) spiders show a prey preference for unparasitized or parasitized LBAM larvae; (3) the

presence of different larval instars of LBAM influences the outcomes of interactions between parasitoids and spiders.

2. Materials and methods

2.1. Insects and spiders

All LBAM larvae and parasitoids used for this study were from laboratory colonies, maintained under controlled room conditions (22 °C, 16L: 8D, 40–60% RH) at the University of California's Insectary and Quarantine Facility in Berkeley, California. The LBAM colony was maintained on a lima bean-based artificial diet developed by Cunningham (2007). Adult parasitoids were held in organo-lysed cages (8 × 11 × 14 cm) with water and honey provided as food; 4th instar larvae were exposed to parasitoids and then provided with diet until parasitoid larvae had developed and emerged for pupation. The female parasitoids used in experiments were 5–10 d old and had no previous oviposition experience (i.e., naïve). Unless otherwise noted, spiders were collected from natural vegetation 48 h prior to being used in experiments; and all were large juveniles.

2.2. Field experiment

The experiment took place at a research facility in Alameda County, California, where 20 field cages (2 × 2 × 2 m; BioQuip, Gardena, CA) were erected along a strip of tilled land ~3.5 m wide × 75 m long that ran from east to west and was bordered by corn fields. The poles at the corner of each cage were pounded ~0.3 m into the ground, and earth was piled on top of the excess mesh around the bottom of the cages to prevent arthropods from escaping. A zipper at the front of each cage provided access during the experiment.

French broom branches (~1 m long) were collected from sites in Alameda County 24 h prior to being used in experiments. The lower portions (~30 cm) of the branches were inserted into 2.8 L water-filled plastic containers, which were buried in the ground at the center of the cages. Numbers of terminal sub-branches on each branch were counted to provide a measure of size and structural complexity, and cages were blocked simultaneously by branch size and position within the study site, before assigning cages to treatments in a randomized complete block design.

The experiment followed a 2 × 2 factorial design, with ten replicates for each of four treatments: control (no spider or parasitoid), only parasitoid (*M. ictericus*) added, only spider (*C. mildei*) added, both parasitoid and spider added. Four female parasitoids and two spiders were added to appropriate cages in an additive-series design, which elevates the total number of natural enemies in the multiple-species treatment. This design is suitable for examining interspecific interactions among natural enemies, since it holds intraspecific interactions constant across different levels of diversity (Schmitz, 2007). Densities of spiders and parasitoids were within the range found in the field (Wang et al., 2012; B.N. Hogg, unpubl.). Branches were inoculated with 30 LBAM larvae (3rd to 4th instar) using a camel-hair brush; smaller stages experienced high background mortality in preliminary field tests, and were not included. Larvae were allowed to acclimate for 24 h before adding parasitoids and spiders. Vials were filled with water and equipped with cotton wicks to provide water to parasitoids, and honey was streaked on the lids of the vials to provide food. Inside each cage, one vial was suspended on a pole beside the plant, and water and honey were refreshed as needed during the trials. Preliminary tests indicated that it would be necessary to prevent spiders from leaving the branches and climbing the cage walls. To this end, 60 cm diameter rings were constructed from

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