



# Host-produced wax affects the searching behavior and efficacy of parasitoids of the giant whitefly *Aleurodicus dugesii* (Hemiptera: Aleyrodidae)

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## ABSTRACT

Insects possess a variety of defenses against natural enemies including physical attack, chemical repellency, physiological suppression, and visual camouflage. The hypothesis that wax production by the whitefly *Aleurodicus dugesii* Cockerell (Hemiptera: Aleyrodidae) functions as a defense against natural enemies was tested using two parasitoid species, *Encarsia noyesi* Hayat (Hymenoptera: Aphelinidae) and *Idioporus affinis* LaSalle & Polaszek (Hymenoptera: Pteromalidae). Parasitoids were allowed to forage on *A. dugesii* nymphs that had their wax either left intact or removed. Percent parasitism and the proportion of time spent grooming and searching were recorded and compared between treatments. There was a significant interaction between wax presence and parasitoid species on observed parasitism. Wax presence appeared to negatively impact *I. affinis* more than *E. noyesi*. In the presence of wax, the percentage of *A. dugesii* nymphs parasitized by *I. affinis* was reduced 30-fold, whereas *E. noyesi* parasitism was reduced 2-fold. Although both species spent more time grooming in the presence of wax, only *I. affinis* spent more time searching. The greater proportion of time devoted to these behaviors by *I. affinis* appeared to be due to its inability to remove wax particles from its body. The results from this study highlight the importance of considering whitefly-produced wax in mediating parasitoid-prey interactions. The differential impact of host defenses must be taken into consideration when selecting candidate natural enemies for biological control programs.

## 1. Introduction

Wax production by insects is widespread and diverse in both form and function (Blomquist and Bagnères, 2010). Functions of insect wax include: maintenance of internal water levels (Ramsay, 1935; Locke, 1965; Hadley, 1981); protection from UV radiation (Pope and Hinton, 1977; Hadley, 1994); epicuticular immunity against microorganisms (Koidsumi, 1957; St. Leger, 1991; Ortiz-Urquiza and Keyhani, 2013); chemical communication (Carlson et al., 1971; Howard and Blomquist, 2005), and protection from the soiling effects of honeydew (Gullan and Kosztarab, 1997; Smith, 1999; Pike et al., 2002).

One of the most intriguing functions of insect wax is its ability to mediate interactions between insect herbivores and their natural enemies. In many situations these waxes appear to serve as a defense against natural enemy attack and, depending on the circumstances, the mode of defense provided has been observed as primary (i.e. one that offers pre-emptive protection) or secondary (i.e. one that offers protection during detection/attack) (Edmunds, 1974). An example of a primary defensive function of insect wax is visual camouflage against natural enemy detection (Moss et al., 2006). Examples of secondary

defensive attributes of insect wax include the physical prevention of feeding by interfering with the proper functioning of natural enemy mouthparts (Eisner, 1994; Völkl and Vohland, 1996; Liere and Perfecto, 2008), acting as a physical barrier against natural enemy attack (Mueller et al., 1992; Agarwala and Yasuda, 2001), chemical repellency of natural enemies (Schwartzberg et al., 2010), and prevention of natural enemy aggression via chemical mimicry of non-prey (Howard et al., 1990; Liepert and Dettner, 1996).

While wax production can benefit the producer, it can also benefit the natural enemies of the herbivore. For example, some natural enemies harvest wax from their prey in order to camouflage themselves from their prey or to protect against intraguild predation (Eisner et al., 1978; Eisner and Silberglied, 1988; Mason et al., 1991). Prey-produced wax can also assist in host seeking behaviors of natural enemies by serving as arrestment cues (van den Meiracker et al., 1990) and ovipositional stimulants (Takabayashi and Takahashi, 1985).

One of the most striking examples of wax production in insects is exhibited by the giant whitefly *Aleurodicus dugesii* Cockerell (Hemiptera: Aleyrodidae). Giant whitefly is an invasive species introduced into the United States from Mexico; it was first discovered in

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Fig. 1. Wax filament bundles (arrow) produced by abdominal plates on an adult female *Aluerodocus dugesii* (left) and wax production by 4th instar *Aluerodocus dugesii* (right).

the United States in 1991 (Hodges, 2004). To date, it is established in at least six states including Texas, California, Arizona, Florida, Louisiana, and Hawaii (Gill, 1992; Nguyen and Hamon, 2002; Heu et al., 2004). Giant whitefly has a broad host range encompassing at least 77 plant genera in 47 families (Bellows et al., 2002; Evans, 2008). Feeding by giant whitefly adults and nymphs deprives their host plants of water and nutrients and, at high infestation levels, can lead to leaf senescence or abscission followed by plant dieback and even death (Bellows et al., 2002). In addition to physical damage to the host plant, giant whitefly adults and nymphs produce copious amounts of wax. This wax affects the aesthetic value of infested plants making giant whitefly a particular nuisance in urban settings.

While the wax produced by adults is noticeable, it is the wax produced by the nymphs which is truly striking. Giant whitefly possesses four nymphal stages; a mobile first instar “crawler” and three sessile stages. The bulk of wax production by nymphs occurs during the 4th instar. Nymphs appear to produce two major forms of wax; long filaments which are produced from two separate rows of five pores each located on the dorsum, and short curls which are produced from numerous dorsal-lateral pores (Fig. 1) (Nelson et al., 2000). Wax filament production by the nymphs gives afflicted leaves a “bearded” appearance, and under natural conditions these wax filaments can attain lengths of 5–20 cm depending on wind conditions (Hodges, 2004).

Little is known on the function of the wax produced by giant whitefly nymphs; however, some have speculated that it may serve as a defense against predators and parasitoids (Nelson et al., 1999). This is of concern as three parasitoid species have been introduced as part of a biological control program against giant whitefly in the United States. They include *Encarsia noyesi* Hayat (Hymenoptera: Aphelinidae), *Idioporus affinis* LaSalle & Polaszek (Hymenoptera: Pteromalidae), and *Entedononecremnus krauteri* Zolnerowich & Rose (Hymenoptera: Eulophidae). Both *E. noyesi* and *I. affinis* forage for hosts on the underside of leaves amongst the nymphs and come into direct contact with their wax. In contrast, *E. krauteri* has the unusual behavior of foraging on the adaxial leaf surface and parasitizes nymphs through the leaf. All three parasitoid species in this system are solitary primary endoparasitoids, with exception of male *E. noyesi* which are produced as hyperparasitoids on immatures of conspecific females (Boughton et al., 2015) or on immature male and female *I. affinis* and *E. krauteri* (pers. obs. EN Schoeller). These parasitoids are koinobionts and emerge during the late “pupal” fourth instar of *A. dugesii* regardless of the instar initially parasitized. No studies have been done examining the reproductive

biology of these species, however *I. affinis* and *E. noyesi* both appear to be synovigenic and possess a clutch of mature eggs two to three days post-eclosion (pers. obs. EN Schoeller). The reproductive biology of *E. krauteri* is still unknown. Adults of all three parasitoid species feed on the honeydew excreted by *A. dugesii*, but only *E. noyesi* has been observed host-feeding on nymphs (pers. obs. EN Schoeller).

The primary objective of this study was to test the hypothesis that wax production by giant whitefly nymphs provides a successful defense against parasitoids. This was achieved by performing a comparative study of the foraging behaviors and parasitism of *E. noyesi* and *I. affinis* in the presence or absence of giant whitefly wax.

## 2. Methods

### 2.1. Plant, Host, and parasitoid material

Plants used to rear giant whitefly were prepared using woody cuttings taken from a single large *Hibiscus rosa-sinensis* ‘White Wings’. Cuttings were placed into a 10 cm pots containing UC Soil Mix Type 3 (Matkin and Chandler, 1957; <http://agops.ucr.edu/soil/>) and grown in environmentally controlled rooms with artificial light (16:8 light:dark photoperiod,  $28 \pm 2$  °C, and ambient RH). Plants were watered every other day and fertilized once a month with a water soluble fertilizer (Growmore®, 20 N-10P-20 K; Gardena, CA). Plants were ready for use five months post-propagation.

Individuals of *A. dugesii*, *E. noyesi* and *I. affinis* used in this study were collected from infested *H. rosa-sinensis* located in Oceanside, CA ( $33^{\circ}10'44.96''N$ ;  $-117^{\circ}22'15.77''W$ ). Infested leaves were brought back to the laboratory and placed into 14 cm diameter ventilated petri dishes. Adult *A. dugesii* and parasitoids on the leaves at the time of collection were immediately removed by aspirating them off of plant material. Adult *A. dugesii* were saved for subsequent use and parasitoids discarded as their ages were unknown. Parasitoid emergence from developing whiteflies was monitored daily and newly emerged parasitoids were placed into 2.5 ml glass vials containing moist cotton and a small piece of honey-soaked tissue (Kimwipes®, Kimberly-Clark Co., Neenah, WI) as an energy source. A total of 10 males and 30 females of each parasitoid species were placed into each vial and then vials were placed into environmental chambers (14:10 L: D photoperiod,  $25 \pm 0.5$  °C,  $70 \pm 10\%$  RH) to allow parasitoids to mate for 48–72 h prior to use.

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