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Parasitism of the glassy-winged sharpshooter, *Homalodisca coagulata* (Homoptera: Cicadellidae): Functional response and superparasitism by *Gonatocerus ashmeadi* (Hymenoptera: Mymaridae)☆

W.L. Chen [a], R.A. Leopold [b,*], M.O. Harris [a]

[a] *Department of Entomology, North Dakota State University, Fargo, ND 58105, USA*
[b] *USDA-ARS Biosciences Research Laboratory, Fargo, ND 58102, USA*

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Abstract

The functional response by the egg parasitoid, *Gonatocerus ashmeadi*, and superparasitism of *Homalodisca coagulata* eggs were found to be related to host age and density when studied under laboratory conditions. Several aspects relating to parasitism of 1-, 3-, 5-, 7-, 9-day-old *H. coagulata* eggs were measured under varied densities ranging from 1:1 to 1:60 parasitoid to host ratios. The functional response for the parasitoid to host eggs of all age groups closely fit the Type II model that describes responses to changing densities. The instantaneous attack rate and handling time of the parasitoid were similar for *H. coagulata* eggs of various ages. The number of host eggs parasitized varies significantly with host density and age, but not when analyzed by a host age × density interaction. However, host age and density, as well as the host age × density interaction, contribute significantly to the differences found in length of the development time of *G. ashmeadi* within host eggs. This parasitoid showed a significantly greater tendency toward superparasitism at parasitoid-to-host ratios ⩽10:100. The maximum number of parasitoid eggs found in a single host egg was 18. The frequencies of superparasitism for *G. ashmeadi* display a random distribution over all observed host densities. Our results also suggest *G. ashmeadi* eliminates the supernumerary parasitoids through physiological suppression.

Keywords: Functional response; Superparasitism; *Gonatocerus ashmeadi*; *Homalodisca coagulata*; Host age and density; Development

1. Introduction

The functional response defines the relationship between the numbers of hosts parasitized per parasitoid with the host or prey density over time (Holling, 1959). The analysis of functional and numerical responses of the parasitoid–host interaction is often used to determine the potential effects of parasitoids on the host population (Oaten and Murdoch, 1975). The effectiveness of a parasitoid in regulating a pest population has been traditionally related to its functional response (Hassell, 1978). Several types of functional responses have been described by models that relate to the rate of predation or parasitism on varying densities and these models may be modified by parameters such as length of exposure to the prey, attack rate, or handling time (Hassell et al., 1977). A Type I model represents a constant linear increase regardless of host density, a Type II model describes an initially constant attack rate which decelerates to a plateau as satiation is reached, a Type III model is typified by a sigmoidal rate increase, and the Type IV model describes a dome-shaped response (Luck, 1985).

☆ Mention of trade names and commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the US Department of Agriculture.

* Corresponding author. Fax: +1 701 239 1348.
E-mail address: leopoldr@fargo.ars.usda.gov (R.A. Leopold).

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Another important attribute for successful parasitoids includes the ability to discriminate between parasitized and non-parasitized hosts (van Lenteren et al., 1978). This ability assists them avoid superparasitism and minimize the waste of time and energy associated with their searching behavior (Godfray, 1994; Mackauer, 1990). Without host discrimination, a solitary parasitoid often superparasitizes one host and causes competition between siblings through physical conflict or physiological suppression. Superparasitism by a solitary parasitoid results in the waste of its eggs, a waste of host searching and handling time, and a developmental delay often accompanied with diminished progeny size. These results usually decrease the efficiency of the parasitoids used in a biological control program. However, superparasitism is also recognized as being adaptive in certain situations (van Alphen and Visser, 1990). The advantages of superparasitism are said to increase the possibility of gaining offspring from a host and to stabilize host–parasitoid interactions in solitary and gregarious parasitoids (van Alphen, 1988; van Alphen and Visser, 1990).

Homalodisca coagulata (Say), the glassy-winged sharpshooter (*GWSS*) (Homoptera: Cicadellidae), has become a great threat to many agricultural and ornamental crops in California of the United States of America because it vectors the xylem-inhabiting bacterium, *Xylella fastidosa* Wells. This bacterium causes Pierce's disease in grapes and similar diseases in numerous other crops (Blua et al., 1999). Recently, *H. coagulata* has become the focus of a major classic biological control program in California (Irvin and Hoddle, 2005). Egg parasitoids in the families Mymaridae and Trichogrammatidae have been released across nine California counties (CDFA, 2003). Among its natural enemies, *Gonatocerus ashmeadi* Girault (Hymenoptera: Mymaridae) is an important species that accounts for 80–95% of the observed parasitism on the sharpshooter eggs in California (Phillips, 2000). In Florida, *G. ashmeadi* is considered as one of the extremely efficient parasitoids of the eggs of *H. coagulata* (López et al., 2004). Previous studies of *G. ashmeadi* have focused on parasitism (Irvin and Hoddle, 2005), overwintering biology (López et al., 2004), mymarid taxonomy (Triapitsyn, 2003; Triapitsyn et al., 1998), and field release investigations (Phillips, 2000). No studies have been conducted to establish the relationship between host densities and rates of attack for *G. ashmeadi*. Moreover, the rates of development and superparasitism of this parasitoid are not known.

The objectives in this study are as follows: (1) to determine the type of functional response of this parasitoid as related to *H. coagulata* eggs of different ages; (2) to assess the frequency of superparasitism in an effort to evaluate whether this parasitoid deposits its eggs in a random or non-random fashion; and (3) to determine the effect of host density and age, and superparasitism with respect to the development and emergence of the parasitoid. It is expected that this information will be useful in assessing the efficiency of *G. ashmeadi* as a biological control agent of *H. coagulata*, devising mass-rearing protocols, and implementing release programs for this parasitoid.

2. Materials and methods

2.1. GWSS colonies

The *H. coagulata* colonies used in this study were originally derived from *GWSS* colonies maintained at the USDA/APHIS Plant Protection Laboratory, Edinburg, TX. All the nymphs were reared in Plexiglass cages ($40 \times 40 \times 60$ cm) on sunflower plants (*Helianthus annuus* L.) in an environmental chamber (25 °C, RH 60%, and 14 L:10D). Fresh plants were introduced each week during the nymphal stages. Upon adult emergence, 70–100 adults were placed into tent-like cages (Bug Dorm-2, BioQuip Products) containing a mixed host system consisting of sunflower (*H. annuus*), an evergreen shrub (*Euonymus japonica* Thunb.), and chrysanthemum (*Chrysanthemum morifolium* L. va. 'White Diamond') plants in a greenhouse augmented with sodium lighting having a photoperiod of 16L:8D. These cultivars were cultured in black plastic pots (11.5 cm diameter × 10 cm high) containing Sunshine soils (Sun Gro Horticulture Canada). The plants were watered daily, and fertilized weekly by using 5% liquid Prolific^{TM} 20-20-20 (Terra International). After 7 or 8 generations, the *GWSS* eggs collected from the colonies in greenhouse were used for the tests.

2.2. Parasitoid rearing

Our *G. ashmeadi* colony originated from a colony maintained at the California Department of Food and Agriculture, Mt. Rubidoux Field Station, Riverside, CA. The parasitoids for these studies were maintained at 22 ± 1 °C on a photoperiod of 10 L:14 D in the plastic tent-cages in the laboratory. Pots of chrysanthemum plants bearing *H. coagulata* egg masses were exposed to the caged *G. ashmeadi* colonies every 15–16 days to maintain a steady supply of parasitoids. Before each test, the euonymus plants bearing 1–3-day-old *GWSS* eggs were exposed to the parasitoid colonies for 24 h to collect parasitized eggs. Upon emergence, the newly emerged wasps were collected every morning and afternoon, and individually put into clean cages. The procedure ensured that all wasps tested were of the same age. These wasps were fed with honey and water, and then at the age of 2 days postemergence, the wasps were used in the tests.

2.3. Functional response studies

The treatment protocols included five host ages (1, 3, 5, 7, and 9 days) and targeted host densities of 10, 20, 30, 40, 50, and 60 *GWSS* eggs per parasitoid female. Embryonic age was determined according to the developmental time of the insects at a constant temperature of 22 ± 1 °C. The petiole of the excised euonymus leaves bearing *GWSS* eggs