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Demographic dynamics of *Platygaster demades* in response to host density

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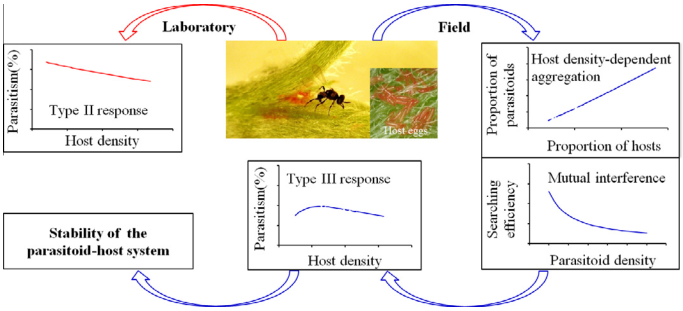
HIGHLIGHTS

- *Platygaster demades* is a hymenopteran parasitoid of the apple leafcurling midge, *Dasineura mali*.
- The wasps display a Type II functional response in the laboratory and a Type III functional response in the field.
- In the field the female wasps aggregate on patches of higher host densities and parasitize more hosts.
- The host density-dependent aggregation raises females' mutual interference and lowers parasitism rate and female progeny.
- The counterbalance between the density-dependent aggregation and mutual interference stabilizes the parasitoid–host system.

GRAPHICAL ABSTRACT



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ABSTRACT

Platygaster demades Walker (Hymenoptera: Platygastridae) is the only hymenopteran parasitoid of apple leaf-curling midge, *Dasineura mali* Kieffer (Diptera: Cecidomyiidae), in New Zealand. Prior to the present study the mechanisms behind the parasitoid–host density interactions were poorly understood. In this study we carried out both laboratory and field experiments to determine the response of *P. demades* to *D. mali* density. In the laboratory, when only a single parasitoid was allowed to forage *D. mali* eggs of a given density, *P. demades* displayed a Type II functional response leading to an inverse density-dependent parasitism. However, *P. demades* showed a Type III functional response in the field where females were able to freely search and disperse between apple shoots infested with *D. mali* eggs of different densities. As a result, the Type III response reflects a more realistic nature of *P. demades* in response to *D. mali* density. Our results also indicate that the numeric response and mutual interference in *P. demades* significantly contributed to the stability of the parasitoid–host system. The density-dependent parasitism in a host range of 50–300 *D. mali* eggs per apple shoot suggests that *P. demades* is highly efficient in controlling *D. mali* populations of the first, third and fourth generations and when necessary, argumentation measures may be taken before the onset of the second generation.

1. Introduction

The functional and numerical responses of parasitoids to host density dynamics and mutual interference among foraging parasitoids are important behavioral characteristics that can be used to assess the potential impact of a parasitoid on the population

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dynamics of its hosts (Kidd and Jervis, 2005). Functional response describes per capita response of a parasitoid to changing host density (Solomon, 1949), and can be categorized into three types (Holling, 1959): Type I, parasitoids search for hosts randomly within a patch and attack hosts at a constant rate, resulting in a linear relationship between the number of hosts parasitized and host density; Type II, the proportion of hosts parasitized by a parasitoid decreases exponentially as the host density increases; Type III, the proportion of hosts parasitized initially increases and subsequently decreases with the increase of host density.

In the natural environment, foraging parasitoids do not always forage singly; instead, they may often encounter other conspecifics (Chong and Oetting, 2006). The numerical response reflects the change in parasitoid density as a function of change in host density (Solomon, 1949; Hassell, 1978) and involves two mechanisms: (1) the aggregational response – a change in parasitoid population due to immigration into an area with increased host density (Readshaw, 1973), and (2) the demographic response – changes in parasitoid reproduction due to changes in host density (Nicholson, 1933). When parasitoids aggregate in patches of high host density, they are more likely to encounter each other while searching for hosts, which in turn may lead to an increased tendency toward dispersal (Hassell, 1978). As a consequence, there is an inverse relationship between the searching efficiency of individual parasitoids and density of parasitoids (Hassell and Varley, 1969). Such behavioral interference between parasitoids can reduce the parasitism rate (Hassell and May, 1973, 1974; Hassell, 1978). Furthermore, after encountering conspecifics, female parasitoids often alter their sex allocation patterns as predicted by local mate competition (Hamilton, 1967), producing more male progeny (Godfray, 1994). Therefore, aggregational response of parasitoids may lead to the mutual interference which in turn may affect the demographic response. These behavioral characteristics may potentially influence the population dynamics in the parasitoid–host systems.

Of 1,135 valid species in the family Platygastridae (Hymenoptera) more than one third (=419) belong to the largest genus, *Platygaster* Latreille (Vlug, 1995; Buhl, 1996; Austin et al., 2005). Most platygastrids attack gall flies, and *Platygaster* are koinobiont egg-larval or egg-pupal parasitoids of Cecidomyiidae (Diptera) (Austin et al., 2005). Apart from a few species attacking economically important pests, the biology of *Platygaster* is poorly understood (Murchie et al., 1999; Austin et al., 2005; Buhl and Notton, 2009).

So far only a few *Platygaster* species have been applied in biological control programs, such as *Platygaster demades* Walker (Todd, 1956), *Platygaster californica* Ashmead (Hopper, 1984), *Platygaster oryzae* (Liu et al., 1982), *Platygaster subuliformis* (Kieffer) (Murchie et al., 1999), *Platygaster hiemalis* Forbes (Rojas et al., 2000), *Platygaster tuberosula* Kieffer (Olfert et al., 2003), *Platygaster robiniae* Buhl and Duso (Duso et al., 2011), and *Platygaster diplosisae* Risbec (Ogah et al., 2011). Most studies on the biological control of flies using *Platygaster* species focus on the parasitoids' development and emergence (Sandanayaka and Ramankutty, 2007; He et al., 2010; Kim et al., 2011; He and Wang, 2011; Son et al., 2013), host searching behavior (Darrouzet-Nardi et al., 2006; Sandanayaka and Charles, 2006; Williams et al., 2007), and phenology and population dynamics with the hosts (Olfert et al., 2003; Duso et al., 2011; He and Wang, 2011;Ogah et al., 2011; Toth et al., 2011). However, how these parameters are related to parasitism levels is still not well understood.

In New Zealand, biological control of the apple leaf-curling midge, *Dasineura mali* Kieffer (Diptera: Cecidomyiidae) using *P. demades* started in the mid 1920's. The parasitoid was introduced from France to control the pear leaf-curling midge, *Dasineura pyri* (Bouché) in 1925 (Miller, 1926) but found to attack *D. mali* (Todd, 1956). The apple midge is a monophagous herbivore that attacks young apple leaves in Europe, North America and New Zealand (Marrison, 1953; Gagné, 1989). Females lay eggs on actively growing shoot tips and larval feeding on the young leaves causes them to roll, producing leaf galls on their outer edges (Todd, 1956; He et al., 2010). *D. mali* is not considered as an important pest in mature apple orchards in New Zealand but fresh fruit contamination by cocooned *D. mali* larvae may cause quarantine problems (Lowe, 1994).

P. demades is the only wasp species known to parasitize eggs of *D. mali*. The parasitoid eggs hatch after *D. mali* larvae start spinning their cocoons in the soil (Todd, 1956; He et al., 2010). The parasitism rate in the field significantly increases as the season progresses from about 50% in the first generation to more than 85% in the fourth generation in New Zealand (He and Wang, 2011). Therefore, this parasitoid can significantly suppress *D. mali* populations in the field and reduce the possibility of fruit contamination. So far, little is known about the parasitism and progeny production in relation to the parasitoid and its host densities, making it difficult to understand the mechanisms behind the parasitism level fluctuations in the field.

Based on the theoretical framework and empirical studies outlined above, we carried out both laboratory and field experiments to test four hypotheses for *P. demades* in the present study: (1) *P. demades* adults exhibit a Type II functional response in the laboratory and a Type III functional response in the field; (2) *P. demades* adults aggregate in response to host density in the field; (3) the proportion of female progeny produced decreases with the increase of both parasitoid and host densities, and (4) the mutual interference due to host density-dependent aggregation promotes the stability and persistence of the parasitoid–host system. In the laboratory we studied functional responses by releasing individual *P. demades* females onto a host patch containing constant numbers of *D. mali* eggs for a constant period of time. In the field we investigated the functional and numerical responses and mutual interference by allowing *P. demades* females to forage on host patches of various densities of *D. mali* eggs.

To our knowledge, this is the first study on the response of a *Platygaster* species to its host density. Information generated here will significantly contribute to our understanding of the foraging behavior and biological control potential of *Platygaster* in general and *P. demades* in particular, under various host densities.

2. Material and methods

2.1. Functional response in the laboratory

A breeding colony of *P. demades* in the laboratory was established from the field-collected mature *D. mali* larvae (third instar) in a mature organic apple orchard (cultivar Tenroy, Royal Gala) in Plant Growth Unit, Massey University, Palmerston North, New Zealand. Larvae were maintained on the rearing medium (vermiculite) in Petri dishes (5.5 cm in diameter × 1.3 cm in height) for pupation at 20 ± 1 °C, 65 ± 5% RH and 15 h day length. Twenty dishes were established with 50 larvae per dish. Newly emerged adults of both *P. demades* (≈20) and *D. mali* (≈50) were released into an aluminum-framed experimental cage (43 × 42 × 40 cm) in which 10 potted apple seedlings (≈20 cm height, bred from rootstock MM 106 FSV) were maintained for oviposition. The cage had a fine metal mesh (aperture size = 0.25 mm) on the back and both sides and Perspex on the top and front and aluminum alloy on the bottom. Parasitoids were reared in the laboratory for three generations to allow them to adapt to the laboratory conditions before used for experiments.

We tested functional responses of the parasitoid to four densities of *D. mali* eggs (50, 100, 200 and 300 per seedling). To obtain the desired host densities, we released about 50, 100, 200, and