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Mutual interference in *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae) when foraging for patchily-distributed light brown apple moth

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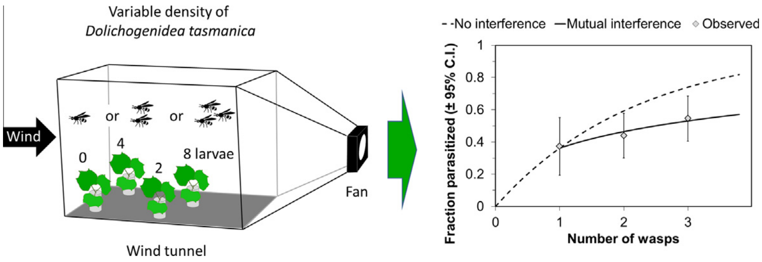
HIGHLIGHTS

- Results are broadly consistent with the predictions of the Ideal Free Distribution.
- Negative relationship between search-efficiency and parasitoid density.
- *D. tasmanica* might deposit a marking pheromone on a visited patch.
- *D. tasmanica* chooses those patches which initially offer the highest oviposition rates.
- As the numbers of foragers increased, they stopped searching more often and earlier.

GRAPHICAL ABSTRACT



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ABSTRACT

Dolichogenidea tasmanica (Hymenoptera: Braconidae) is a solitary endoparasitoid of light brown apple moth (LBAM) and other tortricids that is native to Australia. The foraging behavior of single and multiple female *D. tasmanica* in the presence of patchily-distributed hosts was observed in wind tunnels. Results show that *D. tasmanica* was able to choose those patches which initially offered the highest oviposition rate. Single foragers spent the longest times on patches with higher host densities, but they visited patches with lower host densities sooner in presence of other foragers. The overall rate of parasitism was equalized across patches at the end of the experiment, which indicates that hosts were equally susceptible to attack by *D. tasmanica*, irrespective of their local density. A decrease in the searching efficiency of individual parasitoids with increasing parasitoid density was evidence of interference among female *D. tasmanica*. Nonlinear regression indicates that there was a consistent pattern of mutual interference as wasp density increased and the area of discovery and mutual interference coefficients of Hassell and Varley's (1969) model of parasitoid foraging were estimated as $Q = 0.45$ and $m = 0.526$, respectively. Females chose to visit patches that were not previously visited, which suggests that repellent chemicals were produced by attacked hosts or marking pheromones were deposited by searching females on patches they have visited. This is one factor that can reduce searching efficiency and cause mutual interference among competing *D. tasmanica*.

1. Introduction

There are three basic responses that largely determine the outcome of an insect parasitoid's interaction with its host population.

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They are the response to host density (the functional response), the response to host distribution (the aggregative response) and the response to parasite density (the interference effect) (Hassell and Rogers, 1972; Rogers and Hassell, 1974; Hassell et al., 1976; Cook and Hubbard, 1977). In the field, parasitoids forage in the presence of other conspecifics and several parasitoid females are frequently observed exploiting the same patch of hosts simultaneously (Godfray, 1994). In such cases, the competitive interactions among the foraging parasitoids may reduce per capita search activity and attack efficiency at a given host density (Hassell and Varley, 1969; Waage, 1983). Surprisingly, few studies have investigated foraging strategies under competition (Cook and Hubbard, 1977; Bernstein et al., 1991; Sjerps and Haccou, 1994; Giraldeau and Caraco, 2000; Goubault et al., 2005).

Mutual interference is the combination of behavioral interactions among simultaneously searching parasitoids that causes a reduction in their searching efficiency (Free et al., 1977). The phenomenon of mutual interference was first modeled by Hassell and Varley (1969), who found an inverse relationship between the individual parasitoid searching efficiency and the density of parasitoids. Their analysis showed that mutual interference can play a role in stabilizing parasite–host interactions. Female parasitoids can interfere with each other either (1) directly by fighting, displaying, or hindering competitors (Field et al., 1998; Godfray, 1994; Hardy and Blackburn, 1991; Hardy and Briffa, 2013) or (2) indirectly by modifying their host exploitation strategies (Visser et al., 1990, 1992; Goubault et al., 2005, 2007). Two other forms of interference have been recognized: pseudo-interference and indirect mutual interference. Pseudo-interference (Free et al., 1977) occurs when parasitoids have a non-uniform distribution over patches, which causes variation in the risk of being attacked between individual hosts (Chesson and Murdoch, 1986; Pacala and Hassell, 1991; Hassell et al., 1991). Visser and Driessen (1991) considered changes in sex allocation, clutch size and superparasitm decisions to be indirect mutual interference. All three forms of interference cause a decline in measured parasitoid searching efficiency.

Mutual interference can be represented by a simple mathematical model. It is based on the model of a randomly searching parasitoid (Hassell, 1978):

$$N_a = N_t(1 - e^{aP_t t}) \tag{1}$$

where N_t is the total number of hosts present, N_a is the number of hosts attacked, P_t is the number of searching parasitoids, a is the "area of discovery" which is a measure of searching activity, and t is elapsed time. If mutual interference is assumed to act in a linear manner, then the term aP_t in the random search equation can be replaced by $QP_t^{(1-m)}$ (Hassell and Varley, 1969):

$$N_a = N_t\left(1 - e^{QP_t^{(1-m)}}\right) \tag{2}$$

The coefficient $Q = a$ when $P_t = 1$. This equation can be used to estimate the magnitude of the per-capita effects of mutual interference (m) among searching parasitoids.

In a natural environment it is likely that the spatial distribution of a host population will be patchy and resources will be used by many foragers. This means that foragers are faced with the problem of how to apportion their time among the different parts of the host habitat in order to parasitize the maximum number of hosts in the time available (MacArthur and Pianka, 1966; Cook and Hubbard, 1977; Wajnberg, 2006). Patch time allocation by insect parasitoids has been considered an important behavioral component of host–parasitoid interactions that ultimately influence population dynamics (Hassell and Southwood, 1978; van Alphen, 1988; Basset et al., 2002). Hence, an understanding of patch time allocation is also potentially important in determining the efficacy of parasitoids used in biological control. In other words, an accurate understanding of the mechanisms involved in patch time allocation by parasitoids should lead to a refined ability to select and use effective parasitoid species for pest control (Waage, 1990; Wajnberg, 2006).

Dolichogenidea tasmanica (Cameron) (Hymenoptera: Braconidae) is an endoparasitoid of tortricid species. It is a key biological control agent for the light brown apple moth (LBAM), *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) (Paull et al., 2014). Previously we found that an individual female *D. tasmanica* displays a Type III functional response (Yazdani et al., unpublished results). In this study we observed and analyzed the foraging behavior of single and multiple female *D. tasmanica* in the presence of patchily-distributed hosts. We sought to determine (1) if *D. tasmanica* selectively forages on grape leaves that are more heavily infested by larval LBAM; (2) if their behavior is affected by the presence of competing conspecific females; and (3) the magnitude of any mutual interference among searching individuals that would cause a reduction in the parasitoid's searching efficiency.

2. Materials and methods

2.1. Insects and plants

A laboratory colony of *E. postvittana* was cultured at 22 ± 2 °C and a 12 L: 12 D photoperiod on an artificial diet mainly consisting of lima bean, agar and brewer's yeast. The *D. tasmanica* colony was originally collected from South Australian vineyards and was maintained on infested plantain, *Plantago lanceolata* (L.), with larval LBAM at 23 ± 2 °C and a 14 L: 10 D photoperiod for several generations in the laboratory (for details see Yazdani et al., 2014).

2.2. Patch exploitation strategy and mutual interference

An experiment was conducted to determine if the searching behavior of individual wasps is affected by the presence of other foragers, and how competitors utilized patches infested with varying host densities. The experiment was conducted in four identical wind tunnels with inside dimensions of 35 cm (H) × 50 cm (L) × 30 cm (W). The mean wind speed was 29 ± 0.67 cm/s (mean ± SD) (Yazdani et al., 2014). Each wind tunnel contained four "patches" that consisted of three grape leaves (var Chardonnay; 3.5–4.5 cm L and 4–4.5 cm W). The leaves were placed in a 10 mm diam. × 50 mm glass vial filled with water and the petioles were held together with a piece of clear tape. Each patch of leaves was infested with 0, 2, 4 or 8 s instar LBAM 16–18 h before each experiment. The four different patches were placed randomly in a wind tunnel, 10 cm apart in a square arrangement with in the same order in all wind tunnels of a replicate. 1–2 day old females *D. tasmanica* were released into the wind tunnels, where they were observed for 60 min. In order to stimulate naive wasps to search for hosts, the wasps for each density were exposed to a grape leaf infested with five second instar LBAM larvae for 5 min and allowed to search together and sting larvae. Each wasp was then collected into an 18 mm diam. × 50 mm glass vial and released in the appropriate wind tunnel 10 cm downwind from the first row of patches. After releasing them in all wind tunnels, the locations of wasps were recorded with event-recorder software (The Observer XT, version 11, Noldus, 2012) over 15 min periods that were rotated among wind tunnels. After 60 min the wasps were removed. Leaves from each patch were collected in separate 50 ml plastic cups. On the fourth day after the experiment, the larvae were dissected to determine the frequency of parasitism. This experiment was replicated 16 times, and