



Exposure to competitors influences parasitism decisions in ectoparasitoid fly larvae



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Much theoretical work has been done regarding patch exploitation in insects and several mechanisms have been proposed to describe and predict behaviours under different situations. However, almost no theoretical framework has been developed for parasitoids with host-seeking larvae, even though similar selection pressures are faced by the female of hymenopteran parasitoids and the larvae of dipteran parasitoids. Here we propose and show that factors such as pre-parasitism competition and host physiological state can modulate host orientation and acceptance behaviours in a dipteran parasitoid larva. When larvae were exposed to pre-parasitism competition and then offered different host odours and live hosts, they oriented towards and more readily accepted suboptimal hosts and were more prone to superparasitize. Our results show that the internal state modulates individual decisions that dipteran parasitoids make, confirming the presence of many previously neglected strategies in parasitoids with host-seeking larvae. Hence, comparative studies should be undertaken to form a complete picture of parasitism strategies.

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Patch exploitation strategies in parasitoids have long been studied with both theoretical and experimental approaches. Many theoretical and mathematical models have been developed, with the marginal value theorem (Charnov, 1976), the ideal free distribution (Fretwell & Lucas, 1969) and Waage's (1979) model among the most important. Although useful in starting to understand the principles that rule time allocation to different resource patches by a single individual, the marginal value theorem and the ideal free distribution did not consider behavioural mechanisms mediating patch time allocation or the mechanisms by which animals acquire information about the environment (van Alphen, van Bernstein, & Driessen, 2003; Wajnberg, Bernstein, & van Alphen, 2008). Waage's model attempted to describe the effect of individuals' capacity to obtain information about the quality of the environment leading to increases or decreases in patch time residence (incremental and decremental effects, respectively) after host encounters (van Alphen et al., 2003; Waage, 1979).

Since the publication of these models, many experimental studies have been conducted on insect parasitoids, testing the effects of patch characteristics, female condition, prior visits to host patches and abiotic conditions on patch time allocation (see review by Wajnberg, 2006). Regarding patch characteristics, many studies estimated patch quality by the different number of available hosts, the proportion of healthy hosts, the proportion of different host instars or the presence of competitors in the patch (Wajnberg, 2006). In the majority of studies, patch residence time increased with patch quality. Conversely, when patch quality decreased, behaviour also changed (e.g. shorter patch time residence times and increased acceptance of previously parasitized hosts: Hopper, Prager, & Heimpel, 2013; Outreman, Le Ralec, Wajnberg, & Pierre, 2001).

While this work generated many advances, almost all the theory and experiments were developed for hymenopteran parasitoids where it is the adult female that locates a prospective host and decides whether to use it for ovipositing or host feeding, or to reject it (Godfray, 1994). However, many dipteran and coleopteran parasitoids show a split host-locating strategy where the adult places its eggs near the host and the larvae express active host-seeking behaviour (Brodeur & Boivin, 2004; Feener & Brown, 1997; Godfray, 1994). Since it is the first-instar larvae of dipteran and coleopteran parasitoids that locate the host, they can be viewed as the ecological equivalent of female hymenopteran parasitoids, and

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we expect them to express similar behaviours (Brodeur & Boivin, 2004; Feener & Brown, 1997).

It is well accepted that because there exists a direct relationship between oviposition decisions and fitness, selective pressures should be important in shaping the behavioural mechanisms that determine patch exploitation (van Alphen et al., 2003). Parasitoid females can spread their fitness gain by ovipositing in different hosts. But for a host-seeking larva, the cost of choosing a low-quality host is great because its entire fitness comes from a single host (Brodeur & Boivin, 2004). So, selection pressures might shape the time that larvae spend evaluating host quality much as they do patch searching time for female parasitoids.

The evolution of behavioural mechanisms in parasitoids with host-seeking larvae depends on the distribution of hosts. If hosts are aggregated, the probability of finding more than one host is high. In such conditions, host-seeking larvae may be likely to have evolved discrimination ability (Brodeur & Boivin, 2004). In fact, it has been already shown that host-seeking larvae of different species are capable of locating hosts by means of chemical cues and that host discrimination occurs (Castelo & Lazzari, 2004; Crespo & Castelo, 2009; Goubert, Josso, Lou pre, Cortesero, & Poinso, 2013; L pez, Ferro, & Van Driesche, 1995; Royer, Fournet, Brunel, & Boivin, 1999). In addition to the distribution of hosts, host discrimination could have important adaptive value in species where the host-seeking larvae are long-lived since the probability of finding several hosts in its lifetime is high. However, the effect of host species, size, age, parasitization, instar and nutritional state on host selection by actively seeking first-instar larvae has been little studied and poorly understood.

In addition to patch quality, another source of information that influences patch exploitation is the presence of competitors in the same patch or exposure to competition prior to foraging (Wajnberg, 2006). This information is often used by hymenopteran parasitoids and determines patch residence time and superparasitism depending on its physiological state (Mangel, 1989; Visser, van Alphen, & Nell, 1992). In these cases, a war of attrition is expected where the first female leaving a patch is prone to lose offspring to larval competition if other females remain in the patch and continue to oviposit (Sjerps & Haccou, 1994; van Alphen, 1988). Goubault, Outreman, Poinso, and Cortesero (2005) studied the effect of intraspecific competition in patch residence time in a parasitoid wasp and found that when wasps simultaneously exploited a patch, and hence directly competed, superparasitism increased. They also showed that when wasps had experienced intraspecific competition before the tests, and hence early competition, the proportion of females leaving the patch increased. In the few other studies where the effect of early competition was evaluated, it resulted in an increase of self-superparasitized hosts (Hoffmeister, Thiel, Kock, Babendreier, & Kuhlmann, 2000; Visser, van Alphen, & Nell, 1990; Visser et al., 1992). In the only study where competition has been addressed in host-seeking larvae, the degree of superparasitism increased significantly with the number of foraging conspecifics and the age of the larva when hosts were scarce (Royer et al., 1999).

Given the lack of information on how factors such as host quality (parasitism status and instar) and competition influence individual decisions that host-seeking larvae make, we studied these effects on host location and host acceptance in *Mallophora ruficauda* (Diptera: Asilidae). This solitary ectoparasitoid of the white grub *Cyclocephala signaticollis* (Coleoptera: Scarabaeidae) is a fairly well-studied species with host-seeking larvae. In this species, the adult *M. ruficauda* starts its reproductive stage during early austral summer, but the susceptible host instar (i.e. third larval instar) only becomes available 2 months later (Crespo & Castelo, 2008). Unlike many other parasitoids where the female is responsible for locating

the host, *M. ruficauda* has a split host-location strategy (Castelo, Ney-Nifle, Corley, & Bernstein, 2006). Females lay egg clutches (328 eggs on average) on living plants and also on dry ones in grasslands where adult hosts are present. Females select oviposition sites based on plant height, and parasitism success is highest when eggs are placed on substrates 1.25–1.5 m tall. When the eggs hatch, the larvae are dispersed by the wind and, upon falling to the ground, they bury themselves into the soil. Then, after 1 week in the soil, they moult to the second instar and it is then when the location of the hosts begins (Crespo & Castelo, 2008). *Mallophora ruficauda* parasitizes mainly third-instar hosts of *C. signaticollis* and shows a high preference for this species in the field (Castelo & Corley, 2010). Larvae of *M. ruficauda* can survive 39 days using their own reserves, so the probability of finding several hosts during their life span is high (Crespo & Castelo, 2010). Crespo and Castelo (2009) studied the existence of host discrimination in this species and found that *M. ruficauda* is capable of determining a host's parasitism status (singly parasitized or healthy) by means of chemical cues.

The aim of this study was to determine the effects of hosts of different quality and intraspecific competition on the decisions leading to host location and acceptance. For this, we studied the effect of pre-parasitism competition on the orientation to chemical cues and acceptance of hosts of different quality based on their parasitism status and instar.

METHODS

Insects

We used larval *M. ruficauda* obtained from 1750 egg clutches collected from farms near Buenos Aires, Argentina, in 2010 and 2011. Immediately after egg hatching, neonatal larvae were separated either individually (no competition, NC) in 1.5 ml Eppendorf-type tubes or grouped in flasks (diameter = 5.0 cm; height = 10.0 cm), containing a moistened piece of filter paper as substrate. Grouped larvae were kept at a density of 500 larvae per flask (pre-parasitism competition, PPC). Each flask contained 100 larvae from five different egg clutches, and a total of 350 flasks were used throughout. This density was chosen because it is similar to field conditions (Crespo, n.d.). Drops of mineral water were added when necessary to avoid larvae dehydration. Since these larvae live buried in the soil, tubes and flasks were kept in darkness under controlled temperature ($25 \pm 2^\circ\text{C}$, 60–70% RH) until larvae were used in experiments. Since larvae can live many days in the absence of hosts or any other food source (39 days on average, Crespo & Castelo, 2010), larval age was considered during experiments and only young larvae between 6 and 12 days after moulting to the second instar were used. Each larva was used only once in the experiments and then reared to be released in the field.

Hosts were either killed and used for extraction of their chemical cues in homogenates (host orientation experiments) or kept alive (host acceptance experiments). Host stimuli used in the experiments were obtained from the hindgut of larvae of *C. signaticollis*, which were collected up to a soil depth of 30 cm in grasslands located in the same localities in Buenos Aires province. Hosts were maintained individually under controlled temperature ($25 \pm 2^\circ\text{C}$) in black tubes filled with clean potting soil and fed weekly with fresh carrot pieces. To obtain the attracting stimulus from the host's hindgut, hosts were frozen and, once killed, a homogenate was made using hexane as the extraction solvent following the procedure outlined in Castelo and Lazzari (2004). An equivalent of 2.5 white grubs/ml was used throughout (Crespo & Castelo, 2008, 2009).

We tested the influence of pre-parasitism competition on the orientation to chemical cues and the acceptance of hosts of

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