



Interspecific competition/facilitation among insect parasitoids

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Competition for limited resources is a widespread ecological interaction in animals. In the case of insect parasitoids, species can compete for host resources both at the adult stage as well as at the larval stage. Interspecific competition can play a role in sizing and shaping community structures. In addition of being relevant for basic ecological studies, understanding how interspecific competition between parasitoids affects pest suppression is important for biological control. In this opinion paper we review recent advances in the field of interspecific competition among parasitoids in a biological control perspective. We first discuss adult competition, highlighting which factors are likely to play a role in the outcome of competition when adults interact either directly or indirectly. Then we focus on the interactions occurring between competing larvae that develop within the same host taking also into account the fitness consequences of competition for the larva surviving interspecific competition. We also explore the possibility of interspecific facilitation among parasitoids in those situations in which a given species may benefit from interspecific competition.

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Introduction

Insect parasitoids are key components of terrestrial ecosystems that play an important role in terms of biodiversity, ecological impact and economic importance [1–5]. In a community scenario, insect parasitoids can interact with predators, entomopathogens, other parasitoids and hyperparasitoids [6]. Parasitoids have evolved similar ecological strategies to exploit common host resources; thus the interactions between parasitoid species are likely to be stronger than those established with other organisms.

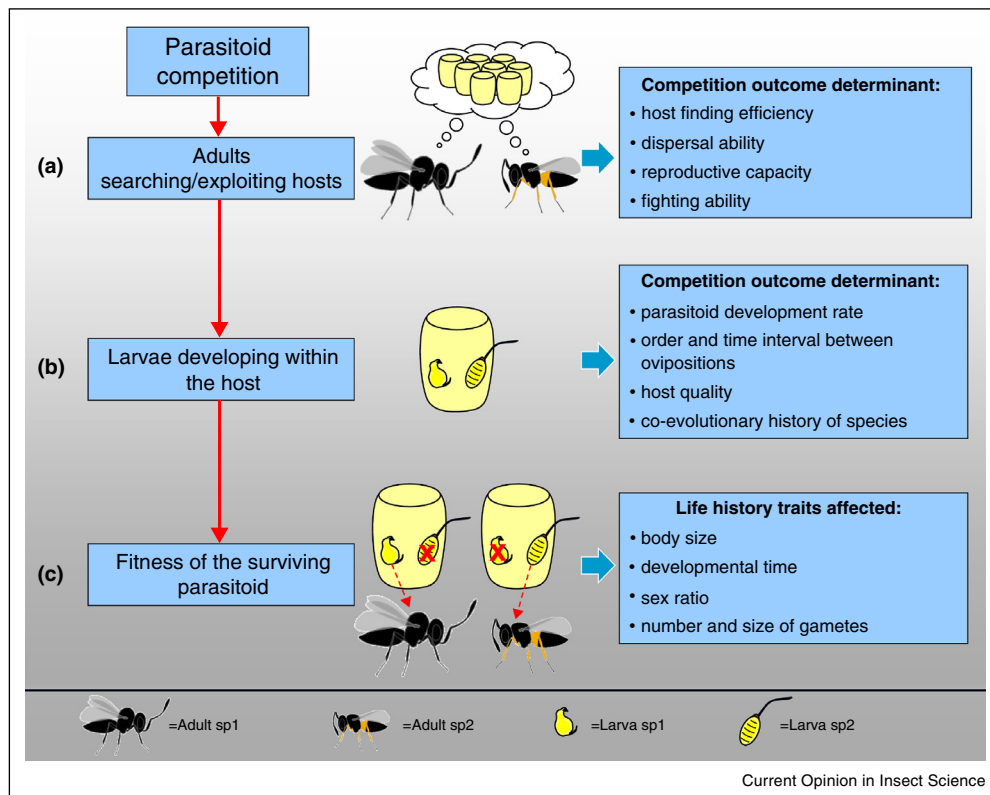
Parasitoids may compete at the adult stage when foraging/exploiting hosts, or at the larval stage, when supernumerary parasitoids develop in the same host (within-host competition) [7,8]. Adult parasitoids can compete for hosts directly, if females are simultaneously present in the same host patch or indirectly, if one female enters a patch that has been previously exploited by another female. In fact, parasitoids are different from predators as the hosts are not immediately removed from the habitat like preys but parasitized hosts remain in situ and can still be exploited by conspecific or interspecific competitors [9].

Several behavioral and ecological traits can affect interspecific competition (Figure 1). The outcome of adult competition between parasitoid species can be mediated by differences in host finding and dispersal abilities, reproductive capacities, fighting abilities and phenological synchronization with the host [10–12,13**]. The outcome of larval competition can be affected by differences in parasitoids' development rates, the stage and physiological status of the attacked host, the order and time interval between ovipositions and the co-evolutionary history of species [14–17]. Interspecific larval competition can impact the development of immature parasitoids as the surviving individual may experience fitness costs or even benefits (interspecific facilitation), due to quantitative and qualitative alterations of the host resources [18,19**,20*]. The purpose of this work is to highlight recent findings in the field of interspecific competition among insect parasitoids focusing on what still needs to be investigated, in our opinion, to advance the understanding of the role played by parasitoid competition in a biological control perspective; thus, we aim to augment the existing framework of the complex pattern of parasitoid competitive interactions outlined by previous reviews [7,8,21–23].

Competition between adult parasitoids

The role played by adult competition among parasitoid species in suppression of pest populations has rarely been considered in a biological control context [23]. Among the several traits that can shape adult competition, the host location efficiency is likely to have a key role (Figure 1a). In insect parasitoids there is a strong selection pressure to optimize foraging strategies due to a direct link between host encounter rate and production of offspring [24]. Consequently, species that display high host location efficiency may have an advantage when competing indirectly with antagonistic species that are also searching in the same habitat. Considering that the vast majority of

Figure 1



Overview of the competitive interactions that can occur between two intraguild parasitoid species. **(a)** Competition at the adult stage and factors affecting the outcome; **(b)** competition at the larval stage and factors affecting the outcome; **(c)** fitness consequence of within-host competition and life history traits affected.

insect parasitoids use semiochemicals to locate their hosts, comparative host location experiments may thus be employed to study the different strategies adopted by foraging adults [7]. To validate this approach, studies on the host location efficiency of competing parasitoid species should be coupled with investigations on parasitism efficiency. For example, laboratory studies on *Trissolcus basalis* and *Ooencyrtus telenomicida*, two parasitoids of *Nezara viridula*, revealed that the former is superior in terms of host finding efficiency, being able to exploit volatile oviposition-induced synomones, and volatile and contact kairomones from adult bugs [25,26] while the latter uses volatile kairomones from adult virgin males [27]. Field investigations on the parasitism efficiency of both species highlighted the importance of host location efficiency in mediating adult competition as *T. basalis* achieved a higher impact on the shared host than *O. telenomicida* despite suffering from interspecific larval competition [28].

When more than one female parasitoid locates the same host patch, they can interact directly through contest behavior for possession of the host. Aggressive interactions can occur in terms of biting, stinging and striking the

intruder [23]. In some species that engage in fighting behavior such as *Goniozus nephantidis*, injuries are not obvious whereas in other bethylid species females can be paralyzed and killed during interspecific contests [23,29–31]. At the intraspecific level, contest outcome can be mediated by several factors including the relative size of the females, the prior ownership status of the host and the egg load of the females [23]. The same factors that regulate contest outcome in intraspecific competition can play a role in interspecific competition; outcomes can be quite asymmetrical due to, for example, the more aggressive species tending to win fights [12]. When competing directly for possession of hosts, parasitoids can also adjust their patch time allocation, and the decision to invest in patch defense instead of leaving the exploited patch to search for other unparasitized hosts is detrimental from a biological control perspective. Patch leaving decision by parasitoids has been intensively investigated in the context of intraspecific competition but very little is known on this topic in terms of interspecific competition. The only experimental work conducted so far suggests that parasitoid species (*Eupelmus vuilleti* and *Dinarmus basalis*) displaying aggressive behavior invest less time in the patch if an interspecific competitor is present than when alone [32*].

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