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Niche breadth and interspecific competition between *Doryctobracon crawfordi* and *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae), native and introduced parasitoids of *Anastrepha* spp. fruit flies (Diptera: Tephritidae)

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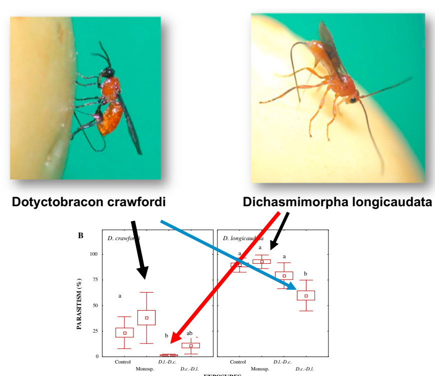
HIGHLIGHTS

- Competitive interactions between two species of fruit fly parasitoids were examined.
- Large niche overlap and strong competition were documented.
- The exotic *Diachasmimorpha longicaudata* outcompeted the native *D. crawfordi*.
- Simultaneous release for augmentative biological control is discouraged.

GRAPHICAL ABSTRACT



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ABSTRACT

Interactions among multiple natural enemies can enhance or interfere with their impacts on host/prey populations. Such could be the case with two species of Braconidae that are currently considered for augmentative biological control of pestiferous tephritid fruit flies in Mexico: the exotic *Diachasmimorpha longicaudata* (Ashmead) and the native *Doryctobracon crawfordi* (Viereck). Since niche overlap and competition could influence the range and effectiveness of these parasitoids were they to be released together, we compared behaviors and morphologies that might influence their access to hosts. These included ovipositor length, diel pattern of oviposition, effect of host instar on development, host range, host-depth, foraging success in different sized host patches, and effects of super- and multi-parasitism. Intra- and interspecific adult interactions on host patches were also observed. There were significant overlaps in ovipositor length, diel patterns of oviposition, preferred host age, and host depth and size. *D. crawfordi* failed to exploit *Anastrepha obliqua* and *Ceratitis capitata*, while *D. longicaudata* parasitized four tephritid species. *D. longicaudata* dominated *D. crawfordi* in multi-parasitism tests and was also better able to survive superparasitism than its competitor. Our results suggest that simultaneous augmentative release of these two species would result in substantial competition. However, because *D. crawfordi*

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is naturally found at greater densities than *D. longicaudata* at high elevations, perhaps because of greater tolerance for cold temperatures, releases in such areas might yield better results than releases of its otherwise superior competitor.

1. Introduction

Interspecific competition among parasitoids can arise through direct aggression or by exploiting a common resource (May and Hassell, 1981; Schoener, 1983; Bográn et al., 2002; Wang et al., 2008), and the greater the similarity among their foraging and oviposition behaviors the greater the scope for competition. In addition, parasitoid competition can occur at two developmental stages, i.e., not only among adults searching for hosts ("extrinsic"), but also among immature stages developing within the same host ("intrinsic") (Vinson and Iwantsch, 1980; Godfray, 1994; Brodeur and Boivin, 2004; Wang et al., 2008).

Fruit flies of the neotropical genus *Anastrepha* support a relatively large guild of larval–pre-pupal opiine braconid parasitoids (Ovruski et al., 2000, 2005; Aluja et al., 2003). While there is considerable scope for competition among them, there has also presumably been selection for adaptations that might limit their mutual interference (e.g., Sivinski et al., 1999). However, two of these species, the exotic *Diachasmimorpha longicaudata* (Ashmead) and the native *Doryctobracon crawfordi* (Viereck), might be particularly apt to adversely affect each other's reproduction because of their gross morphological similarity, and lack of evolutionary history in sympatry. *D. crawfordi* and *D. longicaudata* have the two longest ovipositors in the fruit fly–parasitoid guild (Sivinski et al., 2000), and have been collected from the same fruit species (e.g., *Citrus sinensis* [L.] Osbeck, infested by *Anastrepha ludens* [Loew] and *Psidium guajava* L. infested by *Anastrepha striata* Schiner and *Anastrepha fraterculus* [Wiedemann]) and even from the same individual fruit in a particular tree (Sivinski et al., 1997). Given that both species have been mass-reared for inundative releases in Mexico (Montoya et al., 2000, 2007; Cancino et al., 2008), the potential for competition or mutual interference ("non-additive effects", e.g., Ferguson and Stiling, 1996) if released simultaneously may at best be less effective and at worst have negative agricultural consequences.

D. longicaudata is an oligophagous species (Wharton, 1989), introduced to Mexico in the mid fifties of the last century (Jiménez-Jiménez, 1961). Foraging females respond to fruit size (Sivinski, 1991), color (Vargas et al., 1991) and the odor emitted by fruit (Leyva et al., 1991; Eben et al., 2000; Stuhl et al., 2012). Once on an infested fruit, females detect host larvae through feeding vibrations and sounds (Lawrence, 1981). Only a few aspects of *D. crawfordi*'s biology and ecology are known, largely details concerning altitudinal distribution, host range, apparent lack of diapause, the relationship between ovipositor size and host use, and some demographic parameters related to artificial rearing (Wharton and Gilstrap, 1983; Sivinski et al., 1997, 2000, 2001; Aluja et al., 1998, 2009; López et al., 1999).

Here, our aim was to: (1) reassess ovipositor length for each species to ascertain if there are differences in their potential to reach larvae feeding in fruit pulp (see Sivinski et al., 2000); (2) describe diel patterns of oviposition (as have been noted in other parasitoid species; Atkinson and Shorrocks, 1981, 1984; Vet and van Alphen, 1985), (3) establish the effect of host age (instar) on parasitism rates (Wharton and Gilstrap, 1983; Kraaijeveld et al., 1998), (4) determine the effect of host species (*A. ludens* [Loew], *Anastrepha obliqua* [Macquart], *Anastrepha serpentina* [Wiedemann] and *Ceratitis capitata* [Wiedemann]) on parasitism rates (Sivinski et al., 1997), (5) examine realized fecundity when exposed to different sized host patches (i.e., identical numbers of hosts divided amongst different sized patches) (Walde and Murdoch, 1988; Rosenheim, 1996; Sevenster et al., 1998), (6) determine if females adjust their behavior towards larvae already parasitized by conspecific or heterospecific females (Lawrence et al., 1978), and (7) observe the effects of interspecific interactions on host patches. All of these factors might contribute to, or help avoid, competitive interactions.

2. Materials and methods

2.1. Study sites

Most studies were undertaken on the grounds of the Moscamed facility (SAGARPA-IICA) in Metapa de Domínguez, Chiapas, Mexico. The experiment on the effect of fruit size on parasitism rate was performed at the Instituto de Ecología, A.C., in Xalapa, Veracruz, Mexico. Laboratory conditions at both sites were 24° ± 3 °C and 60–80% relative humidity under a 12 h light:12 h darkness cycle. Temperature and relative humidity were recorded with a hygrothermograph (Oakton Model 08369-70, Cole-Parmer; Chicago, Illinois, USA).

2.2. Insect origin

D. crawfordi were obtained from a colony established from field collected individuals parasitizing *A. ludens* in *C. sinensis* from Llano Grande, Veracruz and subsequently maintained on *A. ludens* larvae (further details on origin can be found in Aluja et al. (2009)). *D. longicaudata* were obtained from a colony reared on *A. ludens* larvae for mass rearing purposes since 1994 (Rull et al., 1995), the colony is refreshed on a yearly basis with field collected individuals and periodically subjected to quality control evaluations that include behavioral traits such as, flight ability, search capacity, and other behavioral aspects (Cancino et al., 2002).

2.3. Parasitoid handling and larval exposure methods

Five-to ten-day-old females of both parasitoid species, all with previous oviposition experience, were used. In Chiapas, these were maintained in wood framed 27 × 27 × 27 cm cages, whereas 30 × 30 × 30 cm Plexiglas cages were used in Veracruz.

Adult parasitoids were fed on honey droplets placed sporadically on cage walls and provided with water. Unless otherwise noted, eight-day-old *A. ludens* larvae were presented to female parasitoids in an oviposition unit described below. In the experiment on the effect of host species on parasitism, we provided *A. ludens*, *A. obliqua*, *A. serpentina* and *C. capitata* larvae. The standard oviposition unit was a Petri dish lid, 10 cm in diameter by 1.5 cm in depth, filled with fresh diet used to rear flies and covered with organdy cloth (Cancino, 1996). The number of larvae in oviposition units ranged from 75 to 200 depending on the particular experiment. In the host depth experiment, organdy cloth replaced the Petri dish lid to create a unit whose depth could be made to vary (e.g., 0.5 and 1 cm). These also contained fresh fly diet. In the experiment to determine the effect of patch