



Intra-host interspecific larval parasitoid competition solved using modelling and bayesian statistics

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ABSTRACT

Intraguild competition is a complex phenomenon that shapes parasitoid communities. When several species of parasitoids oviposit within the same individual host, a complex phenomenon of larval competitive interaction occurs. Within the same guild there is a specialization in competitive strategies, sometimes multiparasitism is avoided, but some species are facultative hyperparasitoids/predators of their competitors.

As these interactions occur within a very small host and during a brief period of time, and that direct observation is very difficult to achieve, we used an alternative methodological approach. We analyzed intraguild host competition mechanisms via the combination of a series of competitive behavioral and functional response models, thurstonian competition model and set theory. These models were fitted via a reversible-jump bayesian model selection procedure to a series of competition experiments data using larvae of three species of *Gonatocerus* spp. (Hymenoptera: Mymaridae), egg parasitoids of the sharpshooter *Tapajosa rubromarginata* (Hemiptera: Cicadellidae) as a case-of-study. This study tests the influence of intrinsic interspecific competition between immature stages within on an individual host, and parasitoid arrival order among the three parasitoid species.

The results showed that the species differed in competitive behavior, some species were better competitors than others. Individuals arriving earlier had a competitive advantage, the weaker species were able to out-compete the stronger ones if the time advantage was longer than 18 h. All the species avoided already parasitized hosts, but in different degrees. The functional response was also different, with the best competitors having shorter estimated handling times. Using this analytical approach on a conventional experimental setup, we gained insights in the mechanism of competition, both on interference and exploitation, and in terms of host selection, all in a single analysis.

1. Introduction

Intraguild competition is a key phenomenon for parasitoid communities (Polis et al., 1989). Most solitary or gregarious endophagous parasitoids require a full host insect to complete their own development (Vinson and Ables, 1980), so, if there are more than one parasitoid species within the same host, a complex phenomenon of competitive interference and predation takes place (Volkoff and Colazza, 1992; Pennacchio and Strand, 2006). Competition between parasitoids can be extrinsic (adult-adult) or intrinsic (adult-larva or larva-larva) (Godfray,

1994).

The analysis of this interaction has two aspects of interest: (1) it helps to understand how parasitoid insect communities are structured and (2) it is important when designing a biological control program, with several controlling species competing with each other. Among the most common difficulties found among studies of competition among parasitoids, are those of observing competition within the host (Harvey et al., 2013). If this is also very small (as in the case of egg parasitoids) and the interactions occur in a very short time, direct observation of this phenomenon is very difficult. Then, complex experimental designs

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and modeling are alternative procedures, being the second option more readily available in the existing infrastructure in the laboratories.

It is known that different species have different competitive strategies, and within the same guild there is a specialization in competition strategies. For example, some species eliminate the competitors via physiological suppression (Chen et al., 2006), other species are facultative hyperparasitoids (Brodeur and Rosenheim, 2000; Hindayana et al., 2001; Lucas, 2005; Cusumano et al., 2011). As a consequence, it has been suggested that interaction between parasitoid guilds should be considered in all biological control programs since competitive effects among them may change the reproductive success of each parasitoid species and thus may affect the host mortality (Nechols et al., 1992; Follett et al., 2000).

Although females of many parasitoid families have the ability to discriminate between unparasitized and parasitized hosts (Wylie, 1965; Van Lenteren, 1981; Ruschioni et al., 2015), in natural systems, multiple species of parasitoids commonly attack the same host (Price, 1971; Hawkins, 1990; Hawkins and Mills, 1996) producing multiparasitism and competition between immature stages (Fisher, 1961; Vinson and Ables, 1980; Cusumano et al., 2011). Multiparasitism occurrence depends on the behavior, reproductive capacity, and phenological synchronization of the female parasitoid with the host (Van Alphen and Visser, 1990; Tumlinson et al., 1993). If the female does not avoid or even prefers a parasitized host, the successful larvae produce adult parasitoids, which changes the population dynamics of the parasitoid species involved and plays a role in sizing and shaping the community (Godfray, 1994).

An interesting approach to analyzing interference competition among parasitoids is the Elo competition model from chess (Elo, 1978) which is already used as a black-box model to analyze animal competitive interactions (Albers and de Vries, 2001; de Vries et al., 2006; Neumann et al., 2011). Intraguild competition between parasitoids may be strongly related to functional response, mostly because the number of hosts attacked depends on the amount available. When there is an excess of hosts, the overlap of different parasitoids within the same host is expected to be less frequent than when their availability is low. If there is an excess of parasitoids, the competition is almost unavoidable. Some authors have combined competition with functional response at population level (Skalski and Gilliam, 2001); and others incorporate interference under intra- and inter-specific competition (de Villemereuil and López-Sepulcre, 2011); yet, no models integrated functional response and behavioral model of the competition process. One problem with these models is their complexity which hinders their analysis. The use of a stepwise model of proposal and selection is a powerful tool to identify the best model that explains a dataset using the fewest parameters possible (Gelman et al., 2003).

Using a novel approach, we analyzed negative interactions between parasitoids (adults and immatures) and their hosts via a series of models, using three egg-parasitoid species as a study-case. For this purpose, we studied the following interactions: indirect extrinsic competition, when two females arrived at the same host at different times regardless of the female detecting if the host was parasitized or not; intrinsic direct competition when a female tried to kill the larvae of other parasitoid species that arrived first to the host; intrinsic direct competition between larvae coming from different species. We conducted black-box laboratory experiments to investigate: (1) the effect of sequential ovipositions of different parasitoid species on the outcome of multiparasitism; (2) the existence of host selection behavior in parasitoid females; (3) the larval competition strength; (4) the effect of interval between ovipositions on the multiparasitism competition outcome. We analyzed the outcome of the experiments by combining functional response models with different variations of the Elo model and set theory.

2. Methods

2.1. Study system

Tapajosa rubromarginata (Signoret) (Cicadellidae: Proconiini), the most frequent and ubiquitous sharpshooter species in Argentina (Paradell et al., 2012), is one of the vectors of the bacteria *Xylella fastidiosa* that causes “Citrus Variegated Chlorosis” (CVC) to Citrus plants (Dellapé and Paradell, 2013). In order to identify biological control candidates to control this vector, we conducted surveys in Argentina between 2003 and 2009, and found 25 species of parasitoid Hymenoptera. During the surveys, we noticed that specimens belonging to three parasitoid families (Mymaridae, Trichogrammatidae, and Aphelinidae) emerged from a single egg mass of *T. rubromarginata*. But the co-emergence of different species of the genus *Gonatocerus*, Mymaridae was more frequent, possibly related to its higher abundance (Logarzo et al., 2004, 2005; Virla et al., 2005, 2009).

2.2. Insect collection and rearing

Laboratory studies were carried out with three egg parasitoids species: *Gonatocerus virlai* (Triapitsyn, Logarzo and de Leon), *G. near tuberculifemur* clade 1, and *G. annulicornis* (Ogloblin) (De León et al., 2008), reared in PROIMI (Planta Piloto de Procesos Industriales Microbiológicos) Laboratory at San Miguel de Tucumán, Tucumán Province. Specimens of *G. virlai* and *G. near tuberculifemur* clade 1 were obtained from egg masses of *T. rubromarginata* collected on Johnson grass (*Sorghum halepense* Pers) in a field at El Manantial (26°49′50.2″S 65°16′59.4″W; elevation 495 m) and San Miguel de Tucumán (26°48′35.7″S 65°16′25.3″W, elevation 470 m) from January to March 2004. *Gonatocerus annulicornis* was obtained from egg masses of the same sharpshooter species on lemon leaves in Horco Molle, Tucumán Province (26°46′50.1″S 65°19′38.3″W; elevation: 703 m) during December 2003. In both areas, parasitoid species were sympatric.

In the laboratory, the colonies were cultured on eggs of *T. rubromarginata* following the methodology established in Virla et al. (2005). Field collected females of *T. rubromarginata* were placed in Polyethylene-Terephthalate (PET) cylindrical vented cages (35 cm high × 18 cm diam.) on lemon plant leaves to obtain host eggs. Potted Citrus lemon plants (pot of 6.3 l) were checked daily for eggs. When egg masses were detected, the sharpshooters and the PET cages were removed, and a leaf with the eggs was ready to be used in the experiments. About 10% of the egg masses were used as control (not parasitized) and maintained until complete development.

All the colonies and the experiments were conducted in the summer at room temperature (26 ± 3°C), at 70–80% RH with natural photoperiod.

2.3. Competition experiment

The experiment consisted of a sequential exposure of leafhopper eggs to parasitoids in an arena which comprised a 10 cm × 1.5 cm culture tube with a cotton plug. An egg mass of *T. rubromarginata* was exposed to the female of one parasitoid species (*G. virlai*, *G. near tuberculifemur* clade 1, or *G. annulicornis*) for 24 hs at the end of which, the female was removed and the egg mass was exposed to a second female of a different species for another 24 hs.

After the second wasp was removed, the exposed egg mass was transferred to a Petri dish with wet tissue paper and covered with clear plastic food wrap to prevent desiccation and to keep wasps from escaping. The egg masses were checked daily and the number of wasps of both species and leafhopper nymphs emerged was recorded. The six possible parasitoid combinations were performed (*G. annulicornis* vs. *G. near tuberculifemur* clade 1; *G. annulicornis* vs. *G. virlai*; *G. near tuberculifemur* clade 1 vs. *G. virlai*, and their reciprocal), 24–58 replicates were conducted (Table 1). As the number of eggs in each egg mass of *T.*

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