



Does host quality dictate the outcome of interference competition between sympatric parasitoids? Effects on their coexistence



Ruth Cebolla, Pablo Bru, Alberto Urbaneja, Alejandro Tena*

Instituto Valenciano de Investigaciones Agrarias (IVIA), Centro de Protección Vegetal, Unidad Asociada de Entomología UJI-IVIA, Moncada, Valencia, Spain

ARTICLE INFO

Article history:

Received 11 October 2016

Initial acceptance 7 December 2016

Final acceptance 6 February 2017

MS. number: 16-00889R

Keywords:

Aonidiella aurantii

Aphytis

armoured scales

competitive exclusion

infanticide

interspecific competition

intrinsic competition

size-mediated interactions

The suitability and quality of herbivorous insect hosts for hymenopteran parasitoids is dynamic, varying with host development. Generally, within a host species, large hosts (i.e. older instars) are considered of higher quality for parasitoid development. Studies of interspecific competition between parasitoids have considered the effect of host instar on indirect competition but its effect on interference competition remains unknown. Here, we report the first results on whether the quality of host instars might dictate the outcome of interference competition between sympatric parasitoids of the genus *Aphytis* (Hymenoptera: Aphelinidae) when they attack low-quality (second) and high-quality (third) instars of their common host *Aonidiella aurantii* (Hemiptera: Diaspididae). Oviposition behaviour (host acceptance and clutch size) in low- and high-quality host instars was similar for both *Aphytis* species in the absence of competition. When they found heterospecific parasitized hosts of high quality, *Aphytis melinus* laid more eggs and accepted significantly more hosts than *Aphytis chrysomphali*, whereas there were no significant differences in the low-quality instar. This result suggests that interference competition is mediated by host quality. However, the progeny proportion of both parasitoids in multiparasitized hosts (outcome of competition) was independent of host quality and *A. melinus* always emerged at higher rates. Therefore, the result of interference competition between these sympatric parasitoids was not affected by host quality and this competition will contribute to the displacement of the native *A. chrysomphali* by the introduced *A. melinus*, which has been observed in some areas of the Mediterranean basin.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Interspecific competition drives community structure and function (Morin, 2011). In extreme cases, stronger competitors can drive weaker competitors to extinction by monopolizing resources (Chesson, 2000). Herbivorous insects are frequently attacked by several hymenopteran parasitoid species whose larvae engage in interspecific competition (Godfray, 1994). Host suitability and quality vary during development and can dictate the outcome of competition among developing parasitoids sharing a host (Harvey, Poelman, & Tanaka, 2013; Price, 1972). Generally, parasitoid species that find and parasitize younger hosts have an exploitative advantage over their antagonists because they can use their host earlier in the season and also because they have a head start in intrinsic competition. This competition among free-living adult parasitoids searching for and using hosts of different instars/sizes is a type of interference competition and has been documented in the field (Bográn, Heinz, & Ciomperlik, 2002; Luck & Podoler, 1985) as

well as in theoretical studies (Briggs, 1993; Harvey et al., 2013; Murdoch, Briggs, & Nisbet, 1996). However, the effect of the host instar/stage on interference competition has never been tested, and we hypothesized that the host instar might facilitate the coexistence of ecological homologue parasitoids when the outcome of competition depends on the parasitized instar/stage.

Several mechanisms related to the behaviour of the mother and/or competition between larvae might explain the apparent instar-related reduction in competitive advantage (Collier, Hunter, & Kelly, 2007; Cusumano, Peri, & Colazza, 2016; Harvey et al., 2013). First, the mother can provide an advantage to its own progeny by killing immature individuals of the competing species or by laying a larger clutch (Cusumano et al., 2016; Tena, Kapranas, García-Marí, & Luck, 2008). We expected this behaviour to vary depending on host suitability and quality, i.e. instar (Hopper, Prager, & Heimpel, 2013). We thus hypothesized that a mother would be less willing to expend energy and time killing progeny of a competitor species in a heterospecific-parasitized host of low quality, i.e. small or young instar. Second, competition between immature parasitoids through either physical contests or a scramble for host resources may also depend on the host instar. For example, parasitoid species

* Correspondence: A. Tena, Centro Protección Vegetal y Biotecnología, Instituto Valenciano de Investigaciones Agrarias (IVIA), Carretera Moncada-Náquera km 4.5, 46113 Moncada, Valencia, Spain.

E-mail address: atena@ivia.es (A. Tena).

with long embryonic development times might have a higher probability of surviving in adult hosts than in young/small hosts in which resources are scarcer. Finally, the outcome might depend on a combination of maternal behaviour and offspring competition.

Here, we studied whether the host instar/stage dictates the outcome of interference competition between parasitoids of the genus *Aphytis* (Hymenoptera: Aphelinidae) and facilitates their coexistence in sympatry in Mediterranean citrus (Pekas, Tena, Harvey, Garcia-Marí, & Frago, 2016; Sorribas, Rodríguez, & Garcia-Marí, 2010). The introduced species *Aphytis melinus* is a superior competitor to the native *Aphytis chrysomphali* as a parasitoid of *Aonidiella aurantii* (Hemiptera: Diaspididae). Their coexistence has been attributed to fluctuating environmental conditions, seasonal variation in parasitoid abundance (Boyer et al., 2014; Pina, 2006; Sorribas et al., 2010) and, more recently, the plasticity of *A. chrysomphali* in exploiting different host instars depending on the *A. melinus* density (Pekas et al., 2016). The latter field study showed that *A. chrysomphali* are recovered in greatest numbers from second-instar hosts, which are poorer quality hosts, when the *A. melinus* density is high and exploits the third instar, a higher quality host (Pekas et al., 2016). However, we hypothesized that this conditional patch partitioning might reflect the fact that *A. melinus* is a superior competitor when both parasitoids parasitize third-instar hosts (high quality), but carries less advantage in second-instar hosts (low quality).

To test our hypothesis and the mechanisms underlying it, we first observed female parasitoids to directly investigate whether females can provide an advantage to their own progeny by laying a larger clutch or killing the progeny of the competitor, depending on the host instar. Then, we analysed the intrinsic competition between parasitoid species to test whether the outcome depends on host instar and/or order of attack (generally, the offspring of the first female have an advantage). Finally, we provide an explanation for the coexistence of *A. melinus* and *A. chrysomphali* in terms of the results obtained here and in a field study (Pekas et al., 2016).

METHODS

System

Parasitoids of the genus *Aphytis* are the most successful and widespread biological control agents of *A. aurantii* in citrus (DeBach & Rosen, 1991; Foster & Luck, 1996; Murdoch, Briggs, & Swarbrick, 2005). These specialist parasitoids can reduce their shared host to levels nearly 200 times lower than the average density observed in their absence (DeBach, Rosen, & Kennett, 1971), suggesting strong resource competition between parasitoid species (Borer, Murdoch, & Swarbrick, 2004). In fact, species of the genus *Aphytis* represent one of the best-known cases of competitive displacement in insects (Luck & Nunney, 1999; Luck & Podoler, 1985; Luck, Podoler, & Kfir, 1982; Pekas et al., 2016; Sorribas et al., 2010). *Aphytis melinus* displaced *Aphytis lingnanensis* (Hare & Luck, 1991) in interior California (Luck & Podoler, 1985; Luck et al., 1982; Podoler, 1981) because the former uses smaller hosts for production of female progeny such that it exploits its hosts before they reach a size suitable for the production of female *A. lingnanensis* (Hudak, 2003; Luck & Nunney, 1999; Luck & Podoler, 1985). Thus, host size represents a resource that is available for the developing parasitoid and is probably the most reliable cue of host quality for *Aphytis* (Hare & Luck, 1991; Pekas, Aguilar, Tena, & Garcia-Marí, 2010). In fact, larger adults of *A. melinus* and *A. chrysomphali* emerge from third-instar hosts than from the second instar; they prefer the third instar when both instars are available, and the immature mortality is slightly lower in the third than in the second instar (Hare & Luck, 1991; Pekas et al., 2010; Pekas et al., 2016; Pina, 2006; Table 2). In the Mediterranean

basin, *A. melinus* has displaced *A. chrysomphali* in some areas, whereas the species coexist in other areas (Sorribas et al., 2010). Although *A. chrysomphali* reproduces parthenogenetically and produces only females when it is infested with the bacterium *Wolbachia* (Pina, 2006), *A. melinus* is considered a superior competitor in the field because it has a higher capacity for dispersion (McLaren, 1976) and is better adapted to climates where citrus is cultivated (Abdelrahman, 1974; Rosen & DeBach, 1979).

Insects

The host herbivore *A. aurantii* was reared on lemons, *Citrus limon*, from a laboratory colony at the Instituto Valenciano de Investigaciones Agrarias (IVIA), Moncada, Valencia, Spain. This colony was initiated in 1999 from scales collected from citrus fields in Alzira in Valencia, Spain, and renewed every 2–3 years with field-collected scales (Tena, Llácer, & Urbaneja, 2013). Approximately two-thirds of the surface of each lemon was covered with red paraffin around the mid-section to retard its desiccation. The red paraffin was prepared with a mixture of 1 kg paraffin pearls (Parafina USP Perlas; Guinama S.L., Alboraya, Spain) and 1 g red pigment (Sudan III; Panreac Química S.A., Castellar del Vallés, Spain). The remaining surface (approximately 24 cm² area) of the lemons was infested by exposure for 48 h to gravid female scales from the *A. aurantii* colony. Once they were infested, lemons were maintained at 27 ± 1 °C at 70 ± 5% relative humidity and darkness until female scales reached the second (9–11 days) and third (19–22 days) nymphal instars, both of which were used in these assays.

Aphytis melinus and *A. chrysomphali* were obtained by exposing third-instar *A. aurantii* on lemons to parasitism by insectary-reared adult wasps maintained in the laboratory at 26 ± 1 °C, 60 ± 5% relative humidity and 16:8 h light:dark cycle. The colonies of *A. melinus* and *A. chrysomphali* were initiated in 2008 and 2013, respectively, from *A. aurantii* scales collected in citrus fields located in the Valencia region of Spain. Both colonies are renewed yearly with field-collected parasitoids.

Between five and 10 late-stage pupae of both parasitoids were removed from parasitized scales and held separately in crystal vials that were 8 mm in diameter and 35 mm long. At emergence, parasitoids were sexed and held in these vials for 1 day to obtain mated females of *A. melinus*. One day after their emergence, females were isolated in the same vials described above, and one *A. aurantii* female body was introduced daily to allow them to feed on a host until they were used 2–3 days later (Heimpel, Rosenheim, & Kattari, 1997). Since *Aphytis* do not obtain sugars from host feeding (Tena, Pekas, Wackers, 2013) and adults die within 3 days without a carbohydrate source (Heimpel et al., 1997), a drop of honey was added on the inside wall of each vial, which was stoppered with a cotton plug. The vials were stored in a climatic chamber (SANYO MLR-350; Sanyo, Japan) at 25 ± 1 °C, 50–70% relative humidity and 14:10 h light:dark.

Experimental Arena

We conducted behavioural observations on a lemon from the colony, where we measured and selected a second-instar scale, of 0.5–0.7 mm², or a third-instar scale, of 0.8–1.0 mm² (Luck & Podoler, 1985; Opp & Luck, 1986; Pekas et al., 2010). To measure the surface of each scale, we used a dissecting microscope with a Leica EC 3 3.1 megapixel digital colour camera (Leica Microsystems GmbH, Spain). Images were processed with Leica LAS EX imaging software for Windows (Leica Microsystems GmbH, Spain) and the areas of the scales (mm²) were measured with ImageJ, a public-domain Java Image-processing program (Rasband, 2016). The

Download English Version:

<https://daneshyari.com/en/article/5538339>

Download Persian Version:

<https://daneshyari.com/article/5538339>

[Daneshyari.com](https://daneshyari.com)