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Is host selection influenced by natal and adult experience in the parasitoid *Necremnus tutae* (Hymenoptera: Eulophidae)?

Nicola Bodino, Chiara Ferracini, Luciana Tavella*

Dipartimento di Scienze Agrarie, Forestali e Alimentari (DISAFA), ULF Entomologia Generale e Applicata, University of Torino, Grugliasco, TO, Italy

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Host selection in parasitoids can be influenced by learning cues obtained during natal and/or adult experience. We investigated the effects of natal and adult host experience on host selection by the indigenous parasitoid *Necremnus tutae* (Hymenoptera: Eulophidae), with an exotic host, the invasive tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae), and a native host, *Cosmopterix pulchrimella* (Lepidoptera: Cosmopterigidae). Colonies of the parasitoid *N. tutae* were reared on the exotic host *T. absoluta* and the native host *C. pulchrimella*, infesting tomato and upright pellitory plants, respectively. Six groups were obtained based on their rearing histories (*T. absoluta* or *C. pulchrimella* larvae) and adult experience (no exposure to host larvae or oviposition experience on the two host species). Parasitoid females of the six groups were tested for behavioural responses to the two host–plant complexes (HPCs) in Y-tube olfactometer assays and in two-choice assays in test arenas. The results suggest that host experience during both natal and adult life may affect the HPC preference of this parasitoid species. In particular, adult experience proved to influence the host preference in both olfactometer and two-choice assays. By contrast, natal experience showed a significant influence on host choice only in naïve parasitoid females in the olfactometer bioassays. In general, the exotic host *T. absoluta*–tomato complex was the odour source preferred by the parasitoid *N. tutae*. The role of natal and adult experience in host-shifting dynamics and how these experiences can combine in adapting mechanisms to a new exotic insect of a generalist parasitoid species are also discussed.

Host selection of insect parasitoids, usually determined by habitat preferences and foraging behaviours, has profound effects on behaviour and fitness of an individual and its progeny (Duan, Messing, & Dukas, 2000; Stamps & Davis, 2006; Vinson, 1998). Besides a heritable component of habitat preference, accumulated experience may affect the subsequent choice of host–habitat complex (Segura, Viscarret, Carabajal Paladino, Ovruski, & Cladera, 2007). Natal experience, i.e. the experience accumulated during the early stages of life before the dispersal phase, can change subsequent habitat preferences of the organism during the dispersal phase. This effect is described by the natalhabitat preference induction (NHPI) theory (Davis, 2008; Davis & Stamps, 2004; Ryan & Bidart-Bouzat, 2014). Similarly, the experience gained during the adult stage may provide mechanisms by which individuals are more likely to select cues related to previous experiences, possibly because they are indicative of the presence of suitable habitat or host food (Davis & Stamps, 2004; Mousseau & Fox, 1998; Ousterhout, Luhring, & Semlitsch, 2014; Papaj & Prokopy, 1989).

Learning from previous experience is one of the main processes involved in habitat choice of a broad range of animals, both vertebrates and invertebrates (Dukas, 2008; Moore, 2004). Among invertebrates, the influence of learning on habitat choice has been demonstrated on *Drosophila melanogaster* over 23–46 generations, highlighting also the importance of learning mechanisms in an evolutionary perspective (Mery & Kawecki, 2004). Learning, if adaptive (i.e. learning that improves the fitness), can affect phenotypic plasticity and in the last instance, drive the evolution of the genetic basis of phenotypic traits (Baldwin effect theory: see Dukas, 2013; Kawecki, 2010; Sznajder, Sabelis, & Egas, 2012). Although its possible influence on adaptation and evolution is widely acknowledged (Dukas, 2013), the role of learning in adaptive responses of natural enemies to new invasive species and in the consequent shift among native and exotic prey/host species has rarely been investigated (Berthon, 2015).

Insect parasitoids represent good model systems to study behavioural ecology and its consequences for evolution, because their search/attack behaviour is strictly related to their fitness,

* Correspondence: L. Tavella, DISAFA, ULF Entomologia Generale e Applicata, University of Torino, largo P. Braccini 2, I-10095 Grugliasco, TO, Italy.
E-mail address: luciana.tavella@unito.it (L. Tavella).

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since the number of parasitized hosts is directly proportional to the number of offspring produced (Godfray, 1994; Hoedjes, Kralemann, van Vugt, Vet, & Smid, 2014; Le Lann et al., 2008; Paur & Gray, 2011; Petitt, Turlings, & Wolf, 1992; Takemoto, Powell, Pickett, Kainoh, & Takabayashi, 2009). Moreover, since the parasitoid offspring are compelled to adapt to the host–habitat complex environmental conditions determined by the mother's choice, the parasitoid female is committed to maximizing her chances of finding and exploiting the host (Godfray, 1994). Therefore, the ability of parasitoid females to learn cues previously experienced can increase the chances of selecting an optimal host, with direct effect on the progeny's fitness (Liu, Xu, Li, & Sun, 2011; Mousseau & Fox, 1998).

Many studies have focused on the precise timing of preference induction during the life stages of insect parasitoids. But if adult learning capabilities have been clearly demonstrated (Hoedjes et al., 2014; Petitt et al., 1992; Takemoto et al., 2009), the effects and especially the timing of the influence of natal experience on adult choices are still debated (Barron, 2001; Colazza & Wajnberg, 2013; Gandolfi, Mattiacci, & Dorn, 2003a; Van Alphen & Bernstein, 2008; Villagra, Pennacchio, & Niemeyer, 2007). Here, we use the broad definition of natal experience of holometabolous insects given by Davis and Stamps (2004), that is the total amount of stimuli received during both preimaginal (i.e. the egg and larval stages) and early adult stage (i.e. recently emerged adult). Therefore, this research focused on the study of the occurrence of preference induction during the predispersal phase (i.e. NHPI).

The behavioural flexibility due to induction/learning capabilities permits the parasitoid to better cope with changes in the environment and community structure (Guerrieri, Pennacchio, & Tremblay, 1997), and can be particularly important when the parasitoid is faced with the arrival of new invasive species (Strauss, Lau, & Carroll, 2006). Although behavioural adaptations play a key role in a successful exploitation of exotic hosts (Wang, Hogg, Levy, & Daane, 2013), the mechanisms that regulate switching from a native to an exotic host by indigenous parasitoids are still unclear (Beckage, 2005; Jones, Bilton, Mak, & Sait, 2015; Strauss et al., 2006) and poorly investigated (Chabaane, Laplanche, Turlings, & Desurmont, 2015; Hassell, 2000; Schönrogge, Stone, & Crawley, 1996).

In this study, we focused on the effects of natal and adult host experience on host selection by an indigenous parasitoid in the Mediterranean area, *Necremnus tutae* (Hymenoptera: Eulophidae), with an exotic host, the invasive tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae) and a native host, *Cosmopterix pulchrimella* (Lepidoptera: Cosmopterigidae). *Necremnus tutae* is a solitary idiobiont parasitoid and the most abundant larval parasitoid associated with *T. absoluta* in the newly invaded areas of the Mediterranean basin (Gabarra et al., 2014; Zappalà et al., 2013). Currently, native hosts of *N. tutae* are not yet known, since this species (formerly reported as *N.* sp. nr. *artynes*) has just recently been described (Gebiola, Bernardo, Ribes, & Gibson, 2015). However, *C. pulchrimella*, a leafminer of upright pellitory, *Parietaria diffusa* (Urticaceae), is reported to be a natural host of the related species *Necremnus artynes* and *Necremnus cosmopterix* (Gebiola et al., 2015; Noyes, 2014). Moreover, individuals of *N. tutae* collected on *T. absoluta* had successfully parasitized and developed on *C. pulchrimella* larvae, thus confirming this species as a possible indigenous host of *N. tutae* (N. Bodino, C. Ferracini & L. Tavella, personal observation).

Previous studies have already found a strong preference of *N. tutae* females for volatiles coming from tomato leaves (either healthy or infested by *T. absoluta* larvae), compared with upright pellitory leaves (either healthy or infested by *C. pulchrimella* larvae; Ferracini et al., 2012). However, *N. tutae* individuals used by Ferracini et al. (2012) were provided by insectaries of a private company (Bioplanet s.c.a., Cesena, Italy), where the parasitoid population was reared on the host *T. absoluta* for several generations, with the possibility of a shift in its natural host preference due to transgenerational NHPI-mediated behaviour (Belda & Riudavets, 2012; Davis & Stamps, 2004; Gandolfi et al., 2003a; Saadat, Seraj, Goldansaz, & Karimzadeh, 2014). Therefore, we analysed the preference and foraging behaviours on the exotic and native host species by *N. tutae* reared and exposed to one of these two hosts during its natal and adult life in olfactometer and two-choice arena experiments. The study aimed to assess whether natal and adult experience can affect the host preference of *N. tutae* towards the host species previously encountered, regardless of whether they are native or exotic. We predicted that both natal and adult host experience could influence the habitat choice (i.e. HPC), increasing the acceptance of the HPCs previously encountered, especially when exposed to the same HPC during both natal and adult stages. In the light of the results obtained, we also discuss the role of host experience in host selection dynamics of a native parasitoid, and how it can influence switching behaviour to a new exotic host.

METHODS

Insect Rearing and Plant Cultivation

Colonies of the exotic host *T. absoluta* were established starting from individuals provided by Bioplanet laboratories (Bioplanet s.c.a., Cesena, Italy). Continuous mass rearing was maintained on tomato plants in cages with an insect-proof net (mesh 680 μm; BugDorm: 60 × 60 × 60 cm, MegaView Science Co., Taichung, Taiwan) for at least 10 generations before the experiments. Tomato seedlings were initially sown in plastic pots (diameter 20 cm), and plants were transplanted individually in pots (diameter 10 cm) after 3 weeks. Tomato plants of the Marmande variety (Green Paradise s.r.l., Milano, Italy) were used for both mass rearing and laboratory trials. Plants used in the experiments had four or five true leaves (14–15 BBCH-scale) and were approximately 60 days old.

Colonies of the native host *C. pulchrimella* were established starting from initial cultures collected on upright pellitory in Piedmont (northwestern Italy), and maintained in screen cages (BugDorm: 47.5 × 47.5 × 47.5 cm) for at least six generations before the experiments. Upright pellitory plants were collected in wastelands, and cuttings were taken to obtain new plants for *C. pulchrimella* rearing. Both *T. absoluta* and *C. pulchrimella* mass rearings were kept in an open-sided greenhouse at 25 ± 3 °C, 50 ± 20% relative humidity and 16:8 h light:dark.

Adults of the parasitoid *N. tutae* were received from Bioplanet, where colonies were established starting from individuals collected on tomato in Sardinia (Italy) in 2009–2010, and then mass-reared on *T. absoluta*–tomato host–plant complex (HPC). Parasitoid mass rearings were conducted on both HPCs, *T. absoluta*–tomato (AT) and *C. pulchrimella*–upright pellitory (AC), and maintained for four to seven generations before starting the experiments. To obtain the adult parasitoids used in the bioassays, additional rearings were set up as follows: about 10 adults (sex ratio ca. 1♀:1♂), from one of the two mass rearings (AT or AC), were released into a Plexiglas cage (40 × 40 cm and 50 cm high) containing the same HPC on which they were reared. After 4 days, parasitoids were removed and plants were transferred into a screen cage (BugDorm: 47.5 × 47.5 × 47.5 cm) for 6 days, allowing parasitoid larvae to conclude their larval development. Plants were then cut and placed in clean Plexiglas cages (35 × 35 × 35 cm) with drops of honey on