

Influence of visual cues on host-searching and learning behaviour of the egg parasitoids *Telenomus podisi* and *Trissolcus basal*s

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Abstract

Insect parasitoids use a variety of chemical and physical cues when foraging for hosts and food. Parasitoids can learn cues that lead them to the hosts, thus contributing to better foraging. One of the cues that influence host-searching behaviour could be colour. In this study, we investigated the ability of females of the parasitoid wasps *Telenomus podisi* Ashmead and *Trissolcus basal*s Wollaston (both Hymenoptera: Scelionidae) to respond to colours and to associate the presence of hosts – eggs of *Euschistus heros* (Fabricius) (Hemiptera: Pentatomidae) – with coloured substrates after training (associative learning). Two sets of experiments were conducted: in one the innate preference for substrate colours was examined, in the other associative learning of substrate colour and host presence was tested in multiple-choice and dual-choice experiments. In the associative learning experiments, *Te. podisi* and *Tr. basal*s were trained to respond to differently coloured substrates containing hosts in two sessions of 2 h each, with 1-h intervals. In multiple-choice experiments, the wasps displayed innate preference for yellow substrates over green, brown, black, or white ones. Even after being trained on substrates of different colours, both parasitoids continued to show preference for yellow substrates. The response to the colours of substrates of both parasitoids was related with the orientation to the plant foliage during the search for hosts.

Introduction

During host localization and recognition, parasitoids use different chemical (semiochemicals) and physical (sound, vibration, colour, size, shape, texture) cues (Vinson, 1985; Fatouros et al., 2008). Semiochemicals play a major role in the host-searching behaviour of insect parasitoids, and a great deal of work has been devoted to this subject in the last 20 years (Vinson, 1991, 1998; Godfray, 1994; Steidle & van Loon, 2002; Fatouros et al., 2008).

Orientation using visual cues, principally colours, for habitat or host detection has been reported for several parasitoid families, such as Aphelinidae, Aphidiidae, Braconidae, Cynipidae, Encyrtidae, Ichneumonidae, and

Pteromalidae (Moreno et al., 1984; Schmidt et al., 1993; Michaud & Mackauer, 1994; Wäckers, 1994; Romeis & Zebitz, 1997; Brown et al., 1998; Oliai & King, 2000; Demas et al., 2002; Fischer et al., 2004; Rouse et al., 2007; Segura et al., 2007; Lucchetta et al., 2008). For egg parasitoids there is less information related to the use of colours during host searching with the exception of some studies on *Trichogramma* spp. (Romeis et al., 1998; Lobdell et al., 2005) and for the egg parasitoid *Ooencyrtus kuwanai* (Howard) (Weseloh, 1972).

Many phytophagous insects have a preference for particular structures of plants to feed or lay eggs (Udayagiri & Welter, 2000; Blackmer et al., 2001); these structures can be told apart by the parasitoids based on colour, allowing them to select (micro) habitats when foraging. The colour of the host can also help the parasitoids in recognition and in gathering information about host quality (Lobdell et al., 2005). In addition, parasitoids could use colours when foraging for food, to guide themselves

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towards flowers to find nectar, or other food resources (Wäckers, 1994)

Host-searching behaviour of parasitoids is influenced by innate behaviour, experience, and associative learning (Vinson, 1998). Innate responses may be modified during adult life through experience, and learning can influence this process (Lewis et al., 1990; Vet et al., 1990). Associative learning is a cognitive process usually related to the use of chemical cues during host searching by parasitoids, which has been documented intensively (Lewis et al., 1990; de Jong & Kaiser, 1991; Papaj & Lewis, 1993; Wäckers & Lewis, 1994; Vet et al., 1995; Du et al., 1997; Meiners et al., 2003; Smid et al., 2007; Huigens et al., 2009).

Stephens (1993) proposed that if the environment is variable, learning will be adaptive. Associative learning enables parasitoids to behave flexibly and confers a selective advantage, allowing them to explore different hosts and reducing environmental uncertainty (Papaj & Lewis, 1993). The ability to learn certain cues may be valuable in parasitoids which must locate inconspicuous hosts (Vet et al., 1991). In parasitoids, learning can happen at different stages of life, e.g., in pre-imaginal stages (Turlings et al., 1993; Gandolfi et al., 2003; Siqueira et al., 2012), in early-adult stages (after emergence from host), or during the adult lifespan (Turlings et al., 1993).

The mechanism of associative learning includes the formation of temporary distinct forms of memory (Smid et al., 2007; Hoedjes et al., 2011). Short-term memory or anaesthesia-sensitive memory is labile and can be disrupted by anaesthesia applied a short time after learning. Another two forms of memory are long term and insensitive to anaesthetic treatment. Anaesthesia-resistant memory (ARM) is consolidated without protein synthesis and is maintained for a few days, whereas long-term memory (LTM) is related to protein synthesis and lasts up to 7 days (Margulies et al., 2005; Bleeker et al., 2006; Smid et al., 2007; van den Berg et al., 2010). For the formation and consolidation of different memory forms, the insects need to be conditioned in different ways. For example, LTM formation requires repeated conditioning events (learning events) separated by intervals, whereas ARM formation could be achieved with massed learning, i.e., a single event or a series of consecutive events (without intervals) (Menzel, 2001; Smid et al., 2007).

As for chemical cues, parasitoids could learn to relate a colour cue with a host or food reward by associative learning (Wardle, 1990; Wäckers & Lewis, 1994, 1999; Oliai & King, 2000; Stireman, 2002; Segura et al., 2007; Lucchetta et al., 2008; Desouhant et al., 2010), but no information on these mechanisms has been reported for egg parasitoids.

As generalist endoparasitoids of stink bug eggs, *Telenomus podisi* Ashmead and *Trissolcus basalis* Wollaston (both Hymenoptera: Scelionidae) are important biological control agents of stink bugs, polyphagous pests that feed on both cultivated and wild plants (Corrêa-Ferreira & Moscardi, 1995; Panizzi, 1997; Laumann et al., 2008). The host-searching behaviour of these parasitoids is strongly influenced by chemical stimuli. They respond to plant volatiles induced by feeding stink bugs (Colazza et al., 2004; Moraes et al., 2005, 2008; Michereff et al., 2011), host sex and alarm pheromones (Mattiacci et al., 1993; Borges et al., 1998; Colazza et al., 1999; Conti et al., 2003; Laumann et al., 2009), and traces left by stink bugs on the substrate (footprints) (Borges et al., 2003). For physical stimuli it is known that these parasitoids also respond to substrate-borne vibratory signals produced during the sexual communication of stink bugs (Laumann et al., 2007, 2011). However, there is no information about the influence of colour during the host-searching behaviour of Scelionidae. The colour of the substrate and of the eggs themselves may be used by the parasitoids to find the hosts. *Telenomus podisi* and *Tr. basalis* parasitize eggs of stink bugs of different colours (yellow, black, green, and brown). These eggs are laid in different structures of the host plants (e.g., pods, stems, and leaves of soybean), which also vary in colour, with different shades of green or brown, depending on the development stage of the plant.

The aim of this study was to investigate both the innate behavioural response to substrate colours of *Te. podisi* and *Tr. basalis* females and their ability to associate the presence of host with colour by associative learning.

Materials and methods

Insects

Euschistus heros (Fabricius) (Hemiptera: Pentatomidae) and parasitoid colonies were started from insects collected in soybean fields near the Embrapa Genetic Resources and Biotechnology Laboratory in Brasília, DF, Brazil (15°47'S, 47°55'W) in 2009–2010. The parasitoids *Te. podisi* and *Tr. basalis* were collected from egg masses of different species of stink bugs found naturally parasitized in field conditions. The insects were kept in an acclimatized room at 26 ± 2 °C, $60 \pm 10\%$ r.h., and a L14:D10 photoperiod, in the Laboratory of Semiochemicals at Embrapa Genetic Resources and Biotechnology, Brasília.

Euschistus heros adults were kept in plastic 8-l cages and fed with seeds of peanut [*Arachis hypogaea* L. (Fabaceae)], soybean [*Glycine max* (L.) Merrill (Fabaceae)], sunflower [*Helianthus annuus* L. (Asteraceae)], and fresh green beans [*Phaseolus vulgaris* L. (Fabaceae)]. Nylon screens (15 cm²) were placed in cages serving as shelter for the

bugs and as substrate for oviposition. The eggs collected daily were placed in Petri dishes (9 cm diameter) and after hatching the nymphs were fed in the same way as adults until they reached the third instar. From this stage the nymphs were transferred to plastic cages containing the diet described previously. To ensure that all the experiments were conducted with eggs of <24 h after oviposition, egg masses were also collected daily for use in the experiments.

Couples of *Te. podisi* and *Tr. basalis* were kept in plastic cages (tissue culture, 25 cm²; ICN Biomedicals, Irvine, CA, USA) capped with a cotton swab. Bee honey was offered as food for adults. Eggs of *E. heros* (<24 h) were offered as hosts and left for 48 h in the cages with parasitoid females to allow oviposition. After this period, the eggs were transferred to another cage of the same dimensions for immature development and hatching. All females used in the bioassays were mated and 24–48 h old. After mating, the females were individually maintained in small glass tubes (7 cm long, 1.5 cm diameter) and fed with a drop of pure honey until use in the experiments.

To reduce the influence of colours on pre-imaginal and early-adult life, the insects were reared in a white environment (walls and racks of the rearing room). Thus, young adult parasitoids had contact only with white (environment) and black (pupae of both species are black) before being used in bioassays.

Experiments: general procedures

All experiments were conducted in an experimental room illuminated with four fluorescent lamps (40 W, 450 lux intensity) at 26 ± 2 °C and $60 \pm 10\%$ r.h. The substrates used were coloured papers (Reipel, Piracicaba, SP, Brazil Colour Set; Yellow no. 418, Green no. 428, White no. 437, Orange no. 420, Brown no. 431, and Black no. 432). The colours were selected to resemble the colours of plant structures (leaves, stalks, flowers) and/or eggs of the stink bugs.

To establish accurately the colour of the substrates used in the experiments, spectral reflectance of substrates was measured (Figure 1) using a spectrophotometer (model USB 2000; Ocean Optics, Dunedin, FL, USA) connected

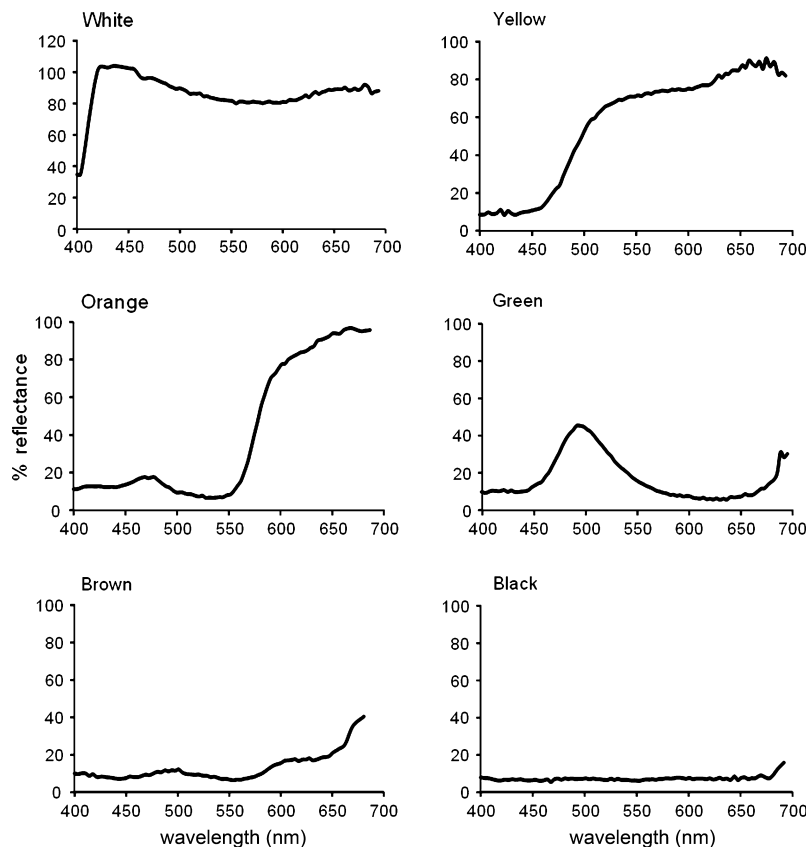


Figure 1 Reflectance spectra of coloured substrates used in the experiments, expressed as reflected light (%) from each substrate in each wavelength relative to a white standard surface (barium sulphate).

to a laptop PC. The measurements were conducted in the room where the bioassays were performed, under the same lighting conditions described above. An optic fibre (R-400-7 UV-VIS; Ocean Optics) connected to the spectrophotometer, captured the reflected light from each substrate, and the reflected spectrum of each coloured substrate was expressed as a percentage relative to a white standard surface (barium sulphate).

Egg masses of *E. heros* ($n = 10$ eggs per mass) used in the experiments were glued with a little drop of arabic gum, to a small piece of paper (0.5×0.5 cm) of the same material and colour as the substrate. Each coloured piece with the egg mass was placed on the centre of the corresponding colour substrate.

The egg parasitoids were introduced into the arena maintaining the tubes in a vertical position to force the insects to walk to the apex of the glass tube and then inverting the tube in the centre area of the arena. In this way the insect were introduced into the experimental arenas with minimal disturbance.

Innate preference

To establish whether there is an innate preference in the response of parasitoids to a specific substrate colour, multiple-choice experiments were conducted in closed arenas made with plastic Petri dishes (14 cm diameter, 2.5 cm high). The arenas were divided into five trapezoidal coloured areas (yellow, green, brown, black, and white) of 7.5 cm^2 . *Euschistus heros* egg masses ($n = 10$ eggs per mass) were placed in the centre of each coloured area (Figure 2A). Each coloured area was placed in the arena separated by 2.8 cm free space, with the sequence of colours determined randomly. The arenas were placed on a rectangular white table illuminated from above as described previously, and the position of the first colour in the sequence of the arena (position 12:00 hours on a clock face) was chosen randomly.

A female of *Te. podisi* or *Tr. basalis* was introduced at the centre of the arena and its colour of choice was recorded. A choice was made when the female remained for at least 10 s in one of the substrates, regardless of whether the female parasitized eggs present in the chosen substrate. Then the female was kept in the arena for a period of 6 h for parasitism. This period was chosen to verify that the female indeed parasitized eggs on the coloured substrate chosen initially and also to check whether the parasitoid could move and parasitize eggs on other substrates. Eighty females of each species of parasitoid were tested.

Associative learning

To test whether the parasitoids could associate the colour of the substrate with a host reward (presence of *E. heros*

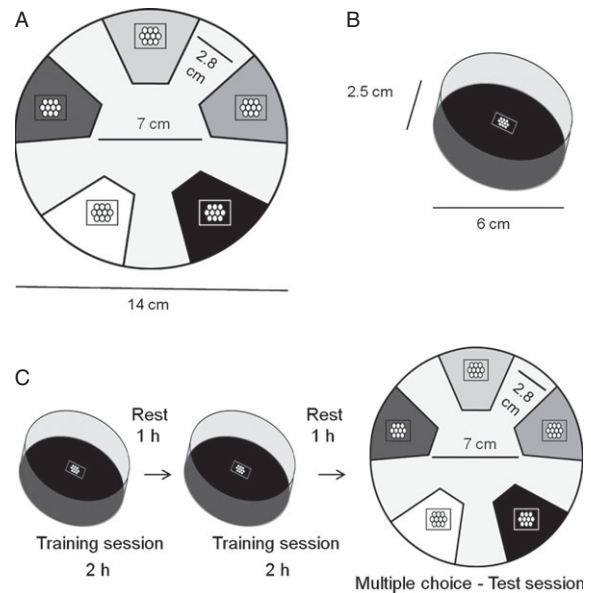


Figure 2 Schematic illustration of the multiple-choice experiments. (A) Top view of the arena (14 cm diameter) used in innate experiment, with five areas and *Euschistus heros* eggs in the centre. (B) Arena (6 cm diameter) used in training session in multiple-choice experiment. (C) Multiple-choice experiment with training and test sessions.

eggs), two sets of experiments were conducted: one offering multiple choices to the parasitoids, after a training period, and the other offering dual choices.

The experiments involved two learning sessions and a test session. Each session lasted 2 h, with 1-h interval between them. In the period between sessions, the females were kept individually in glass tubes (7 cm long, 1.5 cm diameter). During the training sessions, the insects were allowed to parasitize the eggs offered in a substrate of specific colour. In the test session, the initial choice of coloured substrate was recorded, as well as egg parasitism in each substrate. The duration of the training and test sessions and the interval between the trainings and training/test sessions were selected based on biological characteristics of the parasitoids and on previous information about associative learning of colour in parasitoid wasps. In the first 2 days of their adult lifespan, both parasitoids have an oviposition capacity of about 25 eggs per day, *Tr. basalis* parasitizing around 70% of an egg mass (Laumann et al., 2008) and *Te. podisi* around 85% (Pacheco & Corrêa-Ferreira, 1998). Therefore, only two training sessions can be used to avoid total consumption of the egg load by the females. The duration (2 h) was based on the typical time spent by *Te. podisi* and *Tr. basalis* to find and parasitize (including the rest time between ovipositions) 10 eggs in a

small arena such as that used in the bioassays (Aquino, 2011).

The time intervals between training sessions or training sessions and test session were chosen from behavioural observations in our laboratory when the parasitoids were observed in small arenas in the presence of more than one egg mass (MF Aquino, unpubl.); in these situations they usually take some time (from some minutes to a few hours) to pass from the last egg mass parasitized to the next egg mass. In addition, this time of training and intervals used to condition parasitoids to visual (colour) cues is similar to that used by Lucchetta et al. (2008) and Desouhant et al. (2010), who used intervals of 1–2 h between training sessions with visual (colour) cues or between training and test sessions. The experiments were conducted between 08:00 and 20:00 hours, following the period of host searching for both parasitoid species (Borges et al., 1999; Moraes et al., 2005, 2008; Laumann et al., 2008, 2009).

Associative learning: non-dynamic training and multiple-choice test. The females were trained in a Petri dish (6.0 cm diameter, 2.5 cm high) fully lined with black

substrate with an egg mass of *E. heros* ($n = 10$ eggs per mass) in the centre of the arena (Figure 2B). The parasitoid females were introduced at the side of the arena and observed to check egg mass contact and oviposition. After training, females were released in the centre of a multiple-choice arena (mounted as described above) (Figure 2C), and the first choice and the parasitism were recorded. Twenty-five females of each species of parasitoid were tested.

Associative learning: dynamic training and dual-choice test. In these experiments, the parasitoids were trained in arenas of 14.0 cm in diameter (Figure 3A) to allow the parasitoid females to search actively for hosts – i.e., with these arenas, unlike in the ‘non-dynamic training and multiple-choice test’, the females needed to walk around to make physical contact with the egg masses. In the training session, the arenas contained one or two trapezoidal areas of 28.0 cm², and in the test session the arenas contained two areas (Figure 3B). In the arenas with two coloured areas, they were placed at opposite sides and separated by spaces of 7.0 cm. To avoid possible positional effects, the location of the different substrates in

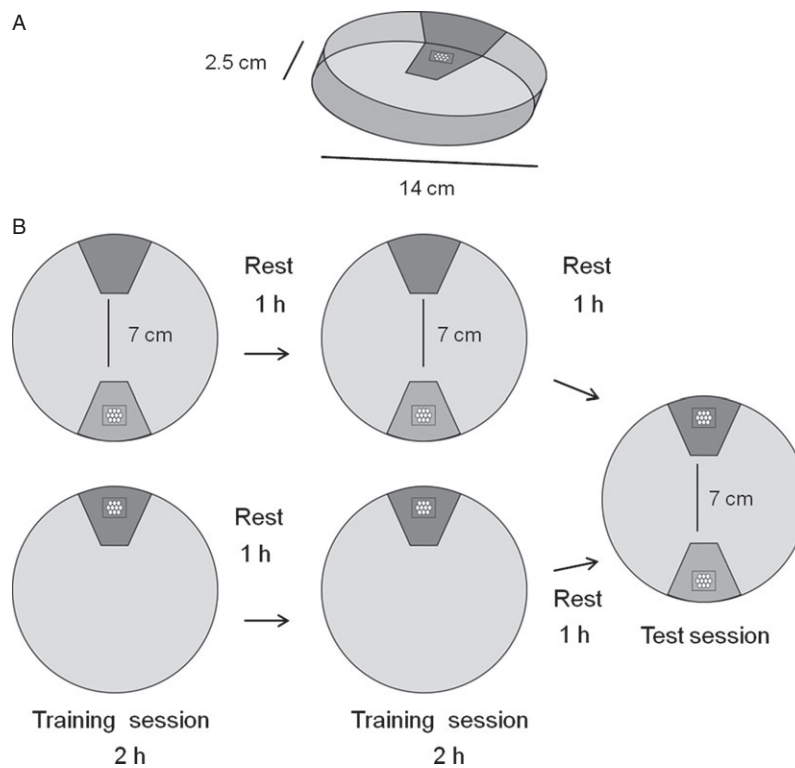


Figure 3 Schematic illustration of the dual-choice experiments. (A) Arena (14 cm diameter) used in experiments. (B) Dual-choice experiment with sequences of training and test sessions. Arenas at the top show the training session in two substrates and arenas below show the training session in only one substrate.

the arenas were alternated between sessions. The parasitoid females were placed in the centre of the arena and their first choice and parasitism were recorded. A series of experiments was carried out as follows: (1) training on orange substrate with host and choice test on yellow and orange substrates, both with hosts; (2) training on green substrate with host and choice test on yellow and green substrates, both with hosts; (3) training on orange (with host) and yellow (no host) substrates and choice test on both substrates with hosts; (4) training on brown (with host) and green (no host) substrates and choice test on both substrates with hosts; and (5) training on green (with host) and brown (no host) substrates and choice test on both substrates with hosts. For each combination of colours 19–25 females of each parasitoid species were tested.

Statistical analysis

In each set of experiments, the choices made by each parasitoid species were analysed by χ^2 test to verify whether the choice of different colours was significantly different from random (all colours with the same chance of being chosen). To assess the influence of colour on parasitism, the number of parasitized eggs in each substrate was compared

using generalized linear models (GLM) and Analysis of Deviance, using a binomial distribution of errors in the models and log as link function; contrast analyses were performed to compare mean differences. All statistical analyses were performed in the 2.10.1 R software (R Development Core Team, 2009).

Results

Innate preference

Both parasitoids preferentially chose yellow substrates, and the black substrates were the least attractive for both species (*Te. podisi*: $\chi^2 = 42.12$, d.f. = 4; *Tr. basalis*: $\chi^2 = 49.62$, d.f. = 4, both $P < 0.001$) (Figure 4A, B). In addition, *Te. podisi* and *Tr. basalis* parasitized more eggs of the yellow substrate compared with eggs placed on the other substrates (Analysis of Deviance z-value = 2533.1 and 3388.2, respectively; contrast analyses: $P < 0.05$) (Figure 4C, D).

Associative learning

Non-dynamic training and multiple-choice test. Even after being trained on black, the female parasitoids preferred the yellow substrate. *Telenomus podisi* parasitized more

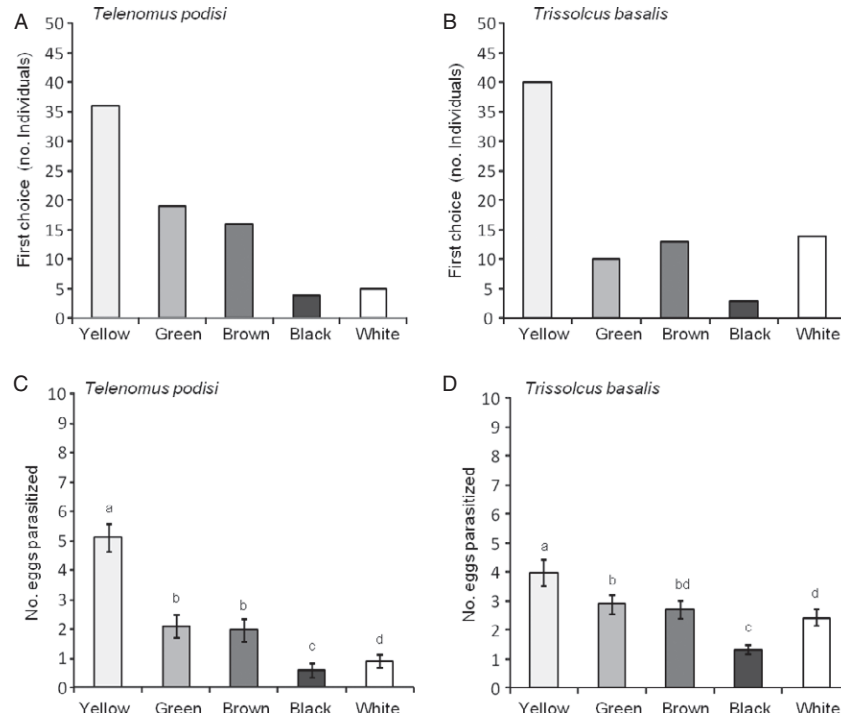


Figure 4 Number of (A) *Telenomus podisi* and (B) *Trissolcus basalis* that chose a colour of substrate in the innate preference experiment. Number of eggs parasitized (mean \pm SE) by female (C) *Te. podisi* and (D) *Tr. basalis* in differently coloured substrates. Mean proportions of parasitism capped with the same letters do not differ significantly (GLM and Deviance analyses followed by contrast analyses: $P > 0.05$).

eggs on yellow substrates than on other colours (Table 1). Although *Tr. basalis* parasitized different numbers of eggs on substrates with different colours, parasitism on yellow substrate differed significantly only from parasitism of eggs on black substrates (Table 2).

Dynamic training and dual-choice test. In this set of experiments, when the training occurred on orange substrates, *Te. podisi* preferred yellow in the test session (Table 1) and *Tr. basalis* did not prefer yellow or orange (Table 2). Parasitism of eggs was higher when placed on yellow substrate for *Te. podisi*, and on orange substrate for *Tr. basalis*. Training on green substrate also indicated preference for yellow. Although preference for yellow was observed in both species, the choice was significant only for *Tr. basalis*, and the parasitism rate was different only for *Te. podisi*, where more parasitized eggs were observed on the yellow substrate (Tables 1 and 2).

When the insects were trained using two coloured areas in the arenas, one with and one without the host, the parasitoids did not associate the colour with a reward in the test session. When the parasitoids were trained in presence of orange (with host) and yellow (without host) substrates the first choice and egg parasitism of *Te. podisi* was oriented to the yellow substrates. Similarly, females of *Tr. basalis* showed no significant preference for substrates on which they were trained (Tables 1 and 2).

When the parasitoids were trained in the presence of brown (with host) and green (without host) substrates the parasitoid females did not display any preference for substrate, although *Tr. basalis* females parasitized more eggs on brown substrate. When the trainings were conducted on substrates of the same colour, but the resource was positioned on the green substrate, only *Tr. basalis* associated the colour with the resource in the test session, preferring the green substrate. In both

Table 1 Initial choice and parasitism of *Telenomus podisi* in experiments of associative learning

Experiment	Test session	First choice					Parasitism			
		No. individuals that chose each colour		n	χ^2	P	n	Number (mean \pm SE)	Statistical test	P
Training on black substrate	Multiple choice (all colours with host)	Yellow	15	25	22.46	<0.001	10	3.52 \pm 0.71a	599.69 ¹	<0.001
		Green	3				10	1.56 \pm 0.31b		
		Brown	3				10	0.72 \pm 0.14c		
		Black	0				10	0.00		
		White	4				10	0.88 \pm 0.17c		
Training on orange substrate (with host)	Dual choice (both colours with host)	Yellow	15	19	6.36	0.01	10	2.26 \pm 0.53	-3.39	<0.001
		Orange	4				10	0.94 \pm 0.22		
Training on green substrate (with host)	Dual choice (both colours with host)	Yellow	15	22	2.90	0.08	10	5.40 \pm 1.18	-3.61	<0.001
		Green	7				10	3.68 \pm 0.80		
Training on orange (with host) and yellow (without host) substrates	Dual choice (both colours with host)	Yellow	18	24	6	0.01	10	5.04 \pm 1.05	-4.71	<0.001
		Orange	6				10	2.91 \pm 0.60		
Training on brown (with host) and green (without host) substrates	Dual choice (both colours with host)	Brown	14	23	1.08	0.29	10	1.82 \pm 0.38	0.00	1.0
		Green	9				10	1.82 \pm 0.38		
Training on green (with host) and brown (without host) substrates	Dual choice (both colours with host)	Green	12	24	0	1	10	2.58 \pm 0.53	1.07	0.28
		Brown	12				10	2.16 \pm 0.45		

¹Multiple-choice analyses were performed with GLM and Deviance analyses followed by contrast analyses, $\alpha = 0.05$; dual-choice analyses were performed with GLM, $\alpha = 0.05$.

Table 2 Initial choice and parasitism of *Trissolcus basalis* in experiments of associative learning

Experiment	Test session	First choice					Parasitism			
		No. individuals that chose each colour	n	χ^2	P	n	Number (mean \pm SE)	Statistical test	P	
Training on black substrate	Multiple choice (all colours with host)	Yellow	10	23	10.26	0.03	10	3.65 \pm 0.77a	1036.8 ¹	<0.001
		Green	3				10	3.47 \pm 0.74a		
		Brown	2				10	3.21 \pm 0.68a		
		Black	2				10	0.91 \pm 0.19b		
		White	6				10	4.13 \pm 0.88a		
Training on orange substrate (with host)	Dual choice (both colours with host)	Yellow	12	19	1.31	0.25	10	4.21 \pm 0.99	2.96	0.003
		Orange	7				10	5.61 \pm 1.32		
Training on green substrate (with host)	Dual choice (both colours with host)	Yellow	17	19	11.30	<0.001	10	2.75 \pm 0.63	-0.80	0.42
		Green	2				10	2.40 \pm 0.55		
Training on orange (with host) and yellow (without host) substrates	Dual choice (both colours with host)	Yellow	11	21	0.04	0.82	10	4.04 \pm 0.90	0.49	0.62
		Orange	10				10	4.28 \pm 0.95		
Training on brown (with host) and green (without host) substrates	Dual choice (both colours with host)	Brown	13	19	1.28	0.25	10	7.52 \pm 1.77	-3.05	0.002
		Green	6				10	6.05 \pm 1.42		
Training on green (with host) and brown (without host) substrates	Dual choice (both colours with host)	Green	19	24	8.16	0.004	10	6.34 \pm 1.35	1.33	0.18
		Brown	5				10	5.73 \pm 1.22		

¹Multiple-choice analyses were performed with GLM and Deviance analyses, followed by contrast analyses, $\alpha = 0.05$; dual-choice analyses were performed with GLM, $\alpha = 0.05$.

cases the colours did not influence parasitism (Tables 1 and 2).

Discussion

The results presented here showed that the parasitoids *Te. podisi* and *Tr. basalis* have an innate preference for yellow substrates. The preference for this colour did not change after conditioning by successful oviposition on egg masses placed on substrates of other colours. The parasitoid females chose the yellow substrate (in the test session) even when *E. heros* egg masses were not present in the training sessions on this substrate. In the experiments of associative learning without yellow substrates, the parasitoids were little influenced by the colour of the substrate.

Hymenopterans have maximum spectral sensitivity for radiations in the range of UV, blue, and green/yellow

(Peitsch et al., 1992; Briscoe & Chittka, 2001). This could explain, from the physiological point of view, the innate response to yellow substrates observed here. Innate response to yellow is also observed in several diurnal insects including many species of hymenopteran parasitoids (Romeis et al., 1998). Yellow surfaces emit radiation in the visible spectral range similar to plant foliage but with greater intensity, as in the substrates used in this work (Figure 1), so to insects yellow could act as a 'super normal foliage stimulus' (Schoonhoven et al., 2005).

Egg parasitoids show innate responses to host-derived cues (Vet et al., 1995). However, innate responses associated with habitat characteristics can be observed when these cues have predictable information related to the presence of appropriate hosts over evolutionary time (Vet et al., 1995). Reflectance in the green/yellow range emitted by the substrate preferred by parasitoids could also represent the use of a cue related to the habitat of the host

(plants). Responses of *Te. podisi* and *Tr. basalis* could be indicative of the use of visual cues by scelionid wasps during the first steps of search and selection of their hosts.

The responses to yellow by insect parasitoids have also been associated with an adaptation for flower foraging because most of the flowering species have yellow flowers (Lucchetta et al., 2008). Adult parasitoids that do not feed on the hosts themselves, as is the case of the insects used here, face a trade-off between searching for hosts or food (Bernstein & Jervis, 2008). Wäckers (1994) showed that when the parasitoid *Cotesia rubecula* Marshall was fed, it preferably focused on the green target, but when the parasitoid was deprived of food it preferred yellow targets, indicating an adaptation to foraging for food (nectar or other sweet substances of flowers). The parasitoids used in this study were not deprived of food, so the preference observed for yellow substrates probably is not a consequence of foraging for food.

In parasitoids, pre-imaginal conditioning can influence the preference by certain cues (Turlings et al., 1993). However, in our experimental set-up parasitoid females cannot have been pre-conditioned to yellow colours. When parasitized, the typical yellow of *E. heros* eggs changes during immature parasitoid development. Initially the eggs become dimmer and during the growth of the parasitoid larva it consumes the yellow yolk and only the transparent chorion remains. When the parasitoid pupae develop, the parasitized egg turns black (Medeiros et al., 1997). The environment in which the parasitoids were reared was predominantly white (walls and racks). In this way, adults emerging from parasitized eggs have early-adult experience with white and black and have not had any contact with yellow or other colours used in the experiments.

The preference for yellow substrates as displayed by both parasitoids could also be related to the egg colour of their preferred hosts. Evidence from laboratory (Sujii et al., 2002) and field studies (Corrêa-Ferreira & Moscardi, 1995; Pacheco & Corrêa-Ferreira, 2000) showed that both parasitoids are oligophagous and can parasitize various species of stink bugs, with egg masses of diverse colours. However, *Te. podisi* prefer the yellow eggs of *E. heros* (Corrêa-Ferreira & Moscardi, 1995; Sujii et al., 2002), and *Tr. basalis* the light yellow to beige eggs of *Nezara viridula* (L.) (Corrêa-Ferreira & Moscardi, 1995; Sujii et al., 2002).

In this study, the parasitoids were not conditioned to recognize the colour of the substrate on which they previously found and parasitized eggs of *E. heros*. Associative learning related to chemical cues commonly occurs in parasitoid wasps (Kaiser et al., 1989; Turlings et al., 1993; Schöeller & Prozell, 2002; Huigens et al., 2009, 2010) and

associative learning has also been demonstrated in relation to colour cues (Wardle, 1990; Wäckers & Lewis, 1994, 1999; Oliai & King, 2000; Lucchetta et al., 2008; Desouhant et al., 2010).

In our experimental set-up, the insect underwent two conditioning trails (training sessions) of 2 h with 1 h these were insufficient to develop either short- or LTM. Some experimental evidence indicated that short-term memory retention in parasitoids is about 1–2 h after oviposition experience (Huigens et al., 2010; van den Berg et al., 2011), so the interval of 1 h used in our experimental set-up could not explain the absence of learning. Long-term memory formation requires repeated conditioning events (usually three learning events) separated by intervals, whereas ARM formation could be achieved with massed learning, i.e., a single event or a series of consecutive events (without intervals) (Menzel, 2001; Smid et al., 2007). Oliai & King (2000) and Van Nouhuys & Kaartinen (2008), each following a different learning protocol, trained *Nasonia vitripennis* Walker and *Hyposoter horticola* (Gravenhorst), respectively, to relate colour cues with rewards in repeated trails during 3–7 days (one trail per day). Lucchetta et al. (2008) trained the parasitoid *Venturia canescens* Gravenhorst to relate colour with food reward after three sessions each, 2 h apart. For scelionid wasps it is known that females could be conditioned to chemical cues by a rewarding experience (successful oviposition). Females of *Tr. basalis* showed stronger arrestment responses to chemical traces (footprints) of stink bugs after oviposition experience in the presence of footprints of *N. viridula* females (Peri et al., 2006). This conditioning response was achieved after a single oviposition experience separated by a 1-h interval of the second contact with chemical traces. This information suggests that the absence of associative learning for colour cues in *Te. podisi* and *Tr. basalis* needs to be checked with other training protocols that include more conditioning sessions or massed learning sessions.

Associative learning in parasitoids has been associated with insects that look for resources in environments that are highly variable in time and space. Parasitoids with complex behaviour must make many choices when searching for hosts, and in these cases, associative learning would be adaptive (Vet et al., 1995). In egg parasitoids, with their short lifetime, limited search capabilities, and high availability of eggs (in comparison to other stages, such as larvae or pupae), associative learning would not be a common strategy for host search (Vet et al., 1995). However, due to eggs being an inconspicuous resource and without many chemicals that offer detectable cues to the parasitoids, several authors have proposed that

associative learning, especially involving semiochemicals from plants, may be a common strategy in the egg parasitoids (Vet et al., 1995; Vinson, 1998; Fatouros et al., 2008).

The spectral reflection pattern of a plant is independent of temperature, speed, and wind direction. It is also relatively constant at variable distances and not substantially altered by air movements, but dependent on light intensity (Schoonhoven et al., 2005). Thus, although there are variations in the intensity of reflection of the substrate, the stimulus can be seen in all directions. However, despite being detectable (large vegetation reflecting green colour), it is not a reliable indicator of the presence of the host. In these cases and as for chemical cues, associative learning could have obvious selective advantage.

In addition, the use of visual cues combined with cues of other modalities (e.g., semiochemicals) in a multimodal fashion may provide better and more reliable information to the parasitoids (Wäckers & Lewis, 1994). This possibility was demonstrated in *Microplitis croceipes* (Cresson) (Wäckers & Lewis, 1994), which show additive effects of visual and olfactory learning. New data appear to confirm that the use of multimodal stimuli could help parasitoids to search in complex environments (Ichiki et al., 2011; Laumann et al., 2011). It remains an open question how scelionid wasps relate colour cues with semiochemicals during the host-searching behaviour.

Our results show that Scelionidae could use colours when searching for hosts. The innate response to yellow substrates in *Tr. basalis* and *Te. podisi* could be related to the region of the visible spectrum in which their receptors respond preferentially (Brown et al., 1998) and may be linked to the orientation to plant foliage during the search for hosts.

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