

# Foraging and associative learning of visual signals in a parasitic wasp

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**Abstract** To cope with environmental variability, animals should gather and use information to reduce uncertainty. In insect parasitoids, associative learning has been widely documented in the context of host foraging. However, despite its potential adaptive value, the insect food searching strategy and cues used to search are poorly understood. In this study, we examined the ability of hymenopteran *Venturia canescens* females to associate food to a visual cue. To broaden the scope of our results, experiments were performed with both arrhenotokous (sexual) and thelytokous (asexual) individuals. The wasps showed innate attraction for yellow and orange stimuli when presented versus blue stimuli. When trained to associate a food reward with one of the attractive colours (orange), they significantly moved from a distance towards the colour previously associated with food. The choice of the innately preferred colour (yellow) was not modified by associative learning. In the context of food foraging, this study is the first to show associative learning using visual stimuli in a parasitoid and active choice of this colour. This ability gives new insights

concerning potential food sources for *V. canescens* in the field, since flowers are sugar sources, which emit colour signals.

**Keywords** Colour learning · Cognitive ecology · Food foraging · Parasitoid · *Venturia canescens*

## Introduction

Most predators and parasitoids forage for patchily distributed resources in fluctuating environments. Acquiring information on resource availability and distribution reduces uncertainty and thus would be selected to match behavioural decisions with the animal's needs and the environmental complexity.

To respond to the metabolic demands of maintenance and reproduction, the two main components of fitness, many parasitoid species feed during their adult life. Some feed on the hosts themselves (Jervis and Kidd 1986; Heimpel and Collier 1996; Gilbert and Jervis 1998; Jervis 1998; Jervis et al. 1996), others, the non-host-feeding parasitoids, feed on nectar and/or honeydew and occasionally on pollen (Leius 1967; Jervis et al. 1993; Jervis and Kidd 1995; Lee and Heimpel 2002; Wäckers and Steppuhn 2003). A number of species feed on both food sources (e.g. Heimpel et al. 1997). Carbohydrates are one of the major components of the parasitoid diet (Gilbert and Jervis 1998; Jervis 1998). Feeding on carbohydrates extends their life expectancy (Siekman et al. 2001; Winkler et al. 2006) and as a consequence, the time available for host searching. Consuming carbohydrates also increases the metabolic reserves required to find new suitable habitats and host patches.

Despite its importance, little attention has been paid to the cues used in the localisation of non-host food sources

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by parasitoids. Flowers are natural targets, where numerous foraging insects including parasitoids find resources like nectar and pollen (Leius 1967; Jervis et al. 1993) and advertise their presence with notable scents and visual stimuli (Wäckers 1994). Olfactory cues have been shown to attract nectar-foragers like pollinators (Raguso 2004). Another important signal emitted by flowering plants is the colour of the corolla, to which insects are attracted because the visual features of flowers contrast with the background (Chittka et al. 1994; Wäckers 1994; Kevan et al. 2001).

Generally, the resources for non-host-feeding parasitoids vary in quantity and quality over both space and time. For instance, honeydew can be of poorer quality when compared with floral nectar in terms of its effect on lifespan (Gilbert and Jervis 1998; Wäckers 2000). Floral nectar is usually of high quality, but its availability fluctuates on a short temporal scale depending on the time of day, climatic conditions and competition with other nectar-foragers (Cruden et al. 1983). Variations in feeding resources also occur between generations, and the quantity and quality of nectar might also depend on the plant species available in the foraging area (Baker and Baker 1983; Kevan and Baker 1983; Kevan 1999).

In these changing environments, flexibility of behaviour is crucial, and learning provides an adaptive mechanism (Stephens 1993; Papaj 1993) to reduce environmental uncertainty. For instance, associating flower colour with the presence of rewards (nectar, pollen) would facilitate resource localisation, thus increasing foraging efficiency (Papaj and Vet 1990; Papaj 1993). Associative learning is a common cognitive process described in host searching by parasitoids. It is, for instance, well known that during successful host location parasitoids learn to associate chemical cues and host reward (Papaj and Lewis 1993; Wäckers and Lewis 1994). Learning based on odours may also be involved in food searching. Females of the parasitoid *Microplitis croceipes* that had experienced an odour during feeding flew preferentially to this odour (Takasu and Lewis 1996). In contrast with this and with the wealth of knowledge available for social Hymenoptera (Giurfa and Vorobyev 1997), associative learning based on visual cues in parasitic Hymenoptera has been scarcely studied, especially in the context of food foraging (but see Wäckers and Lewis 1999 and the Sect. “Discussion”).

The aim of this paper is to test whether, during food foraging, female *Venturia canescens* Gravenhorst (Hymenoptera: Ichneumonidae) are able to learn coloured cues associated with the presence of food. In the field, *V. canescens* females feed on sugary sources like nectar, honeydew or leaf and fruit exudates (Beling 1932; Casas et al. 2003; Desouhant et al. 2005) and access to food results in a significant increase in life-span (Desouhant et al. 2005).

*Venturia canescens* presents two modes of reproduction: arrhenotoky (the common haplo-diploid reproduction in Hymenoptera) and thelytoky (parthenogenetic production of all female offspring, Beukeboom et al. 1999; Schneider et al. 2002). In field conditions, where arrhenotokous reproduction prevails (Schneider et al. 2002), but where thelytokous females are also found (Schneider et al. 2002; Amat 2004), *V. canescens* actively searches for food (Desouhant et al. 2005). Nectar and fruit exudates are potentially abundant, but highly variable food sources. Food is scarce or totally absent in indoor conditions like mills or granaries, where only thelytokous populations thrive. In these conditions, some thelytokous wasps leave the buildings and are found kilometres away from them (J. Lukas and C. Bernstein, personal observations). Casas et al. (2003) showed that thelytokous wasps often feed in natural conditions. This suggests that there are conditions in which asexual wasps engage in food searching, and thus could face the same constraints as their sexual counterparts. Therefore, to broaden the scope of our findings, we studied the associative learning ability of both thelytokous and arrhenotokous *V. canescens*.

Two experiments were conducted. First, a choice experiment was used to test the wasps' innate preference and ability to discriminate between three colours. Then, colour cues were associated with a food reward to test whether *V. canescens* can learn the association.

## Materials and methods

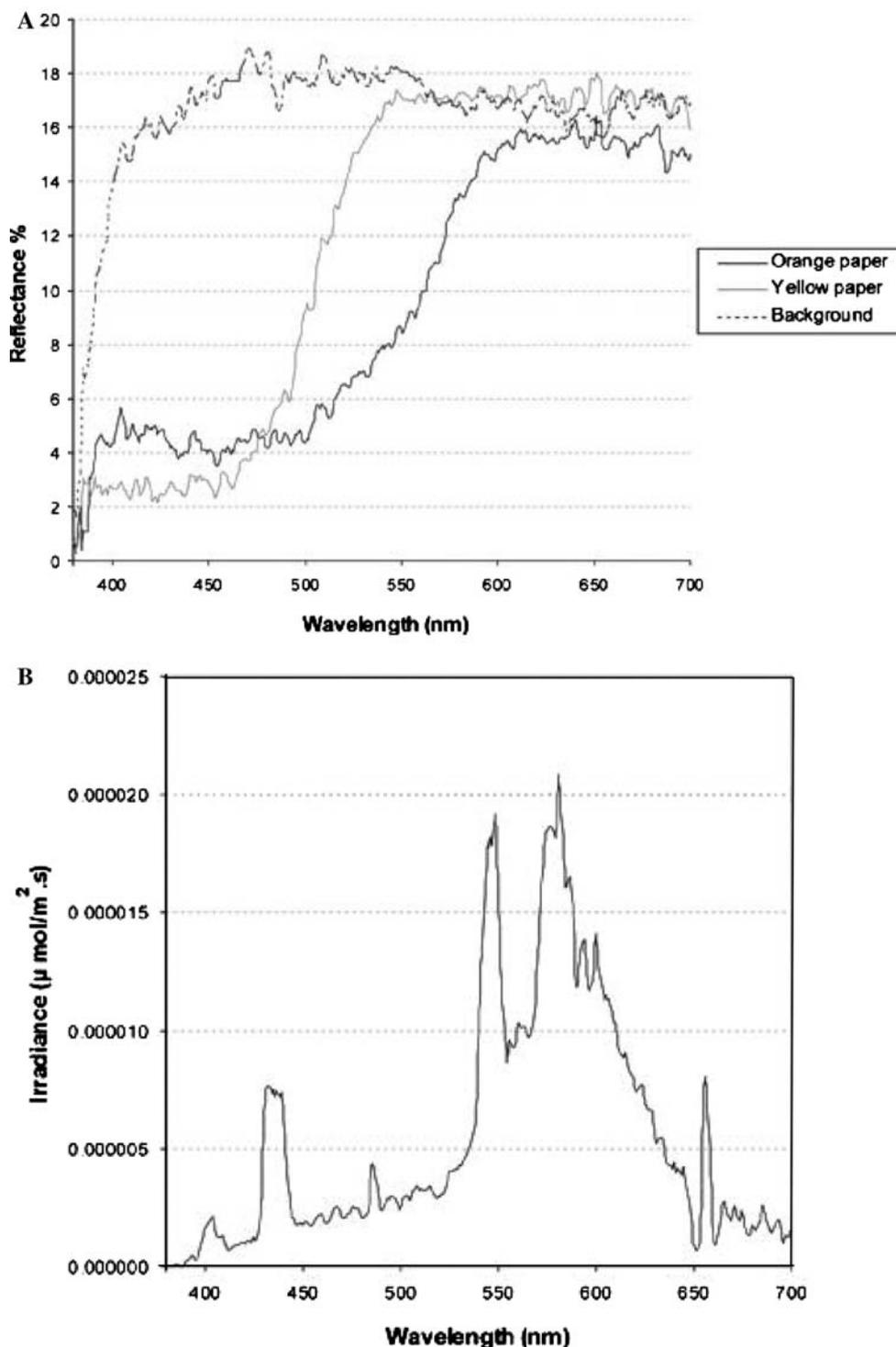
*Venturia canescens* is a non-host-feeding larval endoparasitoid of pyralid moths (Salt 1976) that are a pest in granaries, mills and orchards. This parasitoid is both solitary (only one offspring emerges per host independently of the number of eggs laid on it) and koinobiont (it allows host development after parasitism). Thelytokous females of *V. canescens* have been shown to be capable of associative learning in host-searching activities (Arthur 1971). In laboratory conditions, the wasps use volatile cues to detect food and host sources (Desouhant et al. 2005; Castelo et al. 2003). The wasps used in this study originated from Valence (southeast of France, 44.93°N; 4.90°E), and collected in 2004 in the field. They were reared on the flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) fed on semolina, maintained in a constant environment at  $25 \pm 1^\circ\text{C}$  and  $75 \pm 5\%$  relative humidity, under an artificial light–dark cycle ( $L/D = 12:12$ ). The hosts were originated from a mass rearing facility located in Antibes (INRA), France. Because arrhenotokous wasps exhibit some reluctance to mate under laboratory conditions, the experiments were performed with unmated females.

## Experiment 1: Innate preferences and discrimination of colours

This experiment aimed to determine whether innate preferences for a given colour or colours exist in *V. canescens*. We tested the preference of the insects among three colours: the two, yellow and orange, that were shown to be

the only attractive ones in a previous experience and the one, blue, chosen among the non-attractive colours (Lucchetta 2007). Three dual choice experiments were conducted, between yellow and blue ( $n = 20$  females), orange and blue ( $n = 20$ ) and yellow and orange ( $n = 40$ ). The stimuli consisted of coloured paper sheets (Clairefontaine™ Papers, reflectance spectra are presented in Fig. 1a)

**Fig. 1** **a** Reflectance spectra of the yellow and orange stimuli presented against the white background, and **b** irradiance spectrum of ambient light used in the experiments



positioned at two corners on the same side of a square Plexiglas box (165 mm × 165 mm × 95 mm). The papers were fixed on the outside of the box to avoid any odour effect on choice. The position of the two colours was randomly alternated, and the box was cleaned after each individual test. Females entered the box individually by a 5-mm diameter hole in front of the coloured papers. The room was illuminated with two, 1.2 m long, 36 W white fluorescent tubes covered with a sheet of white filter paper to dim the light and make it more diffuse. We considered that a choice was made when a wasp stayed for at least ten consecutive seconds on one of the coloured corners. Wasps that did not make a choice during 5 min of observation were considered as “indecisive” and were excluded from the statistical analysis.

Wasps were isolated at emergence and kept without food in individual tubes (25 mm diameter × 75 mm height). The trials were carried out 24 h later in a controlled room (25 ± 1°C, 75 ± 5% RH) between 10.00 and 16.00. Because no difference between the two reproductive modes was shown in previous work (Lucchetta 2007), only thelytokous females were tested.

#### Experiment 2: Associative learning between a colour and a food reward

The aim of this experiment was to test the ability of *V. canescens* females to learn a colour signal (used as the conditioning stimulus) associated to a food reward (the unconditioned stimulus). Females of both reproductive modes were first trained to choose between two colours, one being associated with a food reward (training sessions). Then, in a test session, females had to choose between the two colours without the presence of the food reward.

In the training session, females were individually introduced into the same Plexiglas box as in experiment 1, in which two 5 cm diameter Petri dishes were placed in the two corners (on the same side) in front of the hole for individual entrance. One dish contained a few cotton balls drenched with 50% water-diluted honey, whereas the other Petri dish remained empty. Each dish was placed in the corners of the experimental box where the colour stimuli were positioned (see Sect. “Experiment 1”). Each individual experienced three training trials spaced 2 h apart at 10.00, 12.00 and 14.00. When a wasp reached the food patch during training, it was allowed to feed for 10 s. As shown by the behaviour of the animals during the test sessions (all females actively moved towards the colour targets and orange-trained females preferentially moved towards this colour, see Sect. “Results”) this time was long enough to create the association between colour and reward, but short enough to keep a motivation for further food search. Each experimental female was trained to associate yellow

(yellow training) or orange (orange training) with a food reward. Control animals (control training) received a food reward at either colour. The locations of the two coloured papers were reversed between training trials and between the last training trial and the test session. The Plexiglas box was washed and the patches replaced after each trial.

Trained females were tested the same day at 16.00 h, when they had to choose in the same box between the two coloured stimuli in the absence of dishes. We considered that a choice was made when a wasp remained for at least ten consecutive seconds on one of the colour corners. As previously, if after 5 min of observation a wasp did not make a choice, it was considered to be indecisive.

Wasps used were isolated and maintained from emergence in starvation in plastic tubes (75 mm × 20 mm) until the beginning of the training session, 48 h later. Tubes were kept in a controlled environment (25 ± 1°C, 75 ± 5% RH, L:D = 16:8) free of any host or food odours. Experiments took place under the same conditions. Each day of the experiment, the six groups (three learning conditions × two reproductive modes) were tested in a random order ( $N = 168$  in total).

#### Spectral measurements

To ensure that the stimulation parameters were in the frame of the visual sensitivity of Hymenoptera (Peitsch et al. 1992), all the variables concerning light and colour stimuli presented to the animals (colour, brightness) were measured (Fig. 1a). The ambient light spectrum was measured using an Avantes AvaSpec-2048 spectroradiometer calibrated in wavelengths between 290 and 838 nm and a FC-UV600-2-ME optic fibre connected to a CC3 cosine-corrected sensor. Ambient light irradiance was measured in  $\mu\text{mol}/\text{m}^2\text{s}$  using an AVALIGHT-DH-Cal Deuterium–Halogen-calibrated light source (Fig. 1b). Reflectance spectra of the coloured papers through the Plexiglas box and of the white visual background (the walls of the experimental room), were measured at 45° of light incidence using the same spectroradiometer, a FCR-7UV2002-45-ME reflectance probe and a DH-2000 Deuterium–Halogen light source emitting between 215 and 1,500 nm relative to a Spectralon white standard (Fig. 1). Using calculations based on the methods presented in Théry et al. 2005, these measures were analysed in the simulated colour space of Hymenoptera, a technique allowing for more biological realism by approaching the vision of the animal (Théry and Casas 2002). For hymenopteran colour vision, we calculated each colour locus using the model of Chittka (1992) with spectral sensitivity functions of the standard photoreceptors for trichromatic Hymenoptera (Peitsch et al. 1992). These measures indicated that our experimental conditions are adequate for testing associative learning ability since the visual system of females would be

able to discriminate between each colour and the background, and between the two colours presented (see [Appendix](#)). We have computed the colour contrast of the yellow and orange signals against the white background (Euclidean distance in the colour space) and the brightness of the colour stimuli (stimulation of photoreceptors sensitive to green used by Hymenoptera to measure brightness). The results show that yellow is more contrasted against the white background than orange (values of colour contrast are 0.299 and 0.145, respectively). The yellow signal was also brighter than the orange one (excitations of green receptors are 0.472 and 0.368, respectively).

### Data analysis

The choices made by the wasps were analysed by means of a generalised linear model (logit link, binomial distribution of errors with correction for overdispersion when necessary, [Crawley 2002](#)).

The response variable was the proportion of wasps that chose a given colour (experiment 1), or the proportion of wasps that chose the learned colour (experiment 2). The explanatory variables were: the position of the coloured sheets of paper (two modalities left or right, experiment 1); and conditions of training (three modalities: yellow, orange and control), the position of the coloured sheets of paper during the test session and the reproductive mode for experiment 2. Statistical analyses were performed using R software (R Development Core Team [2006](#)).

## Results

### Colour attractiveness and discrimination

The results of experiment 1 show a significant innate preference for yellow rather than an orange stimulus (coloured papers). Out of the 40 wasps tested, 34 made a choice for a colour and of these, 23 were attracted to yellow (58%) and 11 to orange (28%) ( $\chi^2 = 4.23$ , 1 *df*,  $P = 0.039$ ). Out of 20 females given the choice between yellow and blue, 15 made a choice: 14 preferred yellow (70%) and one was

attracted by blue (5%) ( $\chi^2 = 11.27$ , 1 *df*,  $P < 0.0008$ , [Fig. 2](#)). The wasps are less attracted by blue or orange stimuli. When they had to choose between these two colours, only eight out of 20 made a choice: seven for the orange signal (35%) and only one for the blue signal (5%) (Binomial test,  $H_0$ : probability = 0.5,  $P = 0.035$ ).

The position of the paper sheets did not influence the choice made by the wasps (global effect of the position of the learned colour,  $\chi^2 = 1.204$ , 1 *df*,  $P = 0.273$ ). The discrimination between two innate attractive colours, yellow and orange, allowed us to use these two colours in the learning experiment.

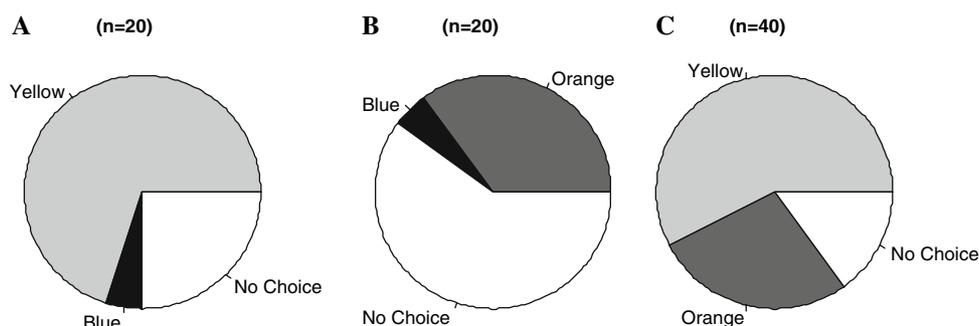
### Associative learning between colour and food reward

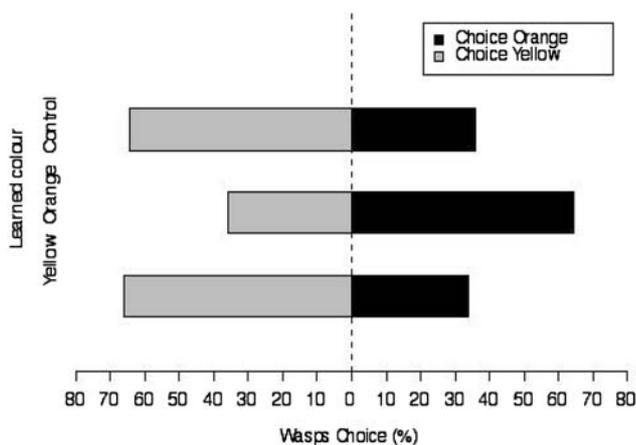
Since there was no difference between wasps of the two reproductive modes ( $\chi^2 = 0.65$ , 1 *df*,  $P = 0.42$ ) and the location of the colours did not influence the choices made by the wasps ( $\chi^2 = 2.13$ , 1 *df*,  $P = 0.14$ ), we pooled the data of all individuals. There were no significant interactions between any factors. None of the 168 wasps were indecisive during the test session.

The results show the ability of *V. canescens* to learn a colour (orange) associated with a food reward. When females were conditioned to find food associated with an orange stimulus (*orange training*), they preferentially chose this colour in the test session (36 out of 56 wasps, 64%), while 36% (20 out of 56) of the females in the *control training* group (i.e. conditioned with food associated with both colours) were attracted by this colour ([Fig. 3](#)). The difference in preference for orange between the two training conditions is significant ( $\chi^2 = 9.27$ , 1 *df*,  $P = 0.002$ ).

Out of 56 females conditioned to yellow (*yellow training*) 37 (66%) chose the learned colour in the test session. The proportion of females that chose yellow is not significantly different from that observed for the females in the *control training* group ( $\chi^2 = 0.04$ , 1 *df*,  $P = 0.84$ ) and reflected the innate preference (67%) for yellow over orange. The comparison between the proportion of orange-trained wasps and those trained to yellow that chose orange also yielded a significant difference ( $\chi^2 = 10.49$ , 1 *df*,  $P = 0.001$ ).

**Fig. 2** Innate preferences and colour discrimination in *V. canescens* females: Proportion of chosen colour when wasps were presented with yellow versus blue (**a**), orange versus blue (**b**) and yellow versus orange (**c**) paper sheets. The proportion of indecisive wasps is represented in white





**Fig. 3** Conditioned colour choice with food reward: mean proportion of yellow or orange choice during the final test according to the learning conditions (food associated with yellow, orange or both in the control group)

## Discussion

*Venturia canescens* females show innate preferences for certain (yellow coloured) stimuli. They also have the ability to learn an orange-coloured stimulus associated with a food reward. In this case, when the females had the choice between two colour stimuli, they significantly chose to move towards the colour previously associated with a food source, even if this colour was placed opposite to the innately preferred one. Thelytokous and arrhenotokous wasps do not differ in their ability to learn to associate food to a given colour.

*Venturia canescens* was already known to feed on sugary resources in field conditions (Casas et al. 2003) and to use olfactory cues to locate food (Desouhant et al. 2005). Our results give new insights into the signals used and the cognitive process implicated in food searching. They show that food searching is an active process that involves associative learning of visual signals. The results also indicate that nectar-bearing flowers might constitute a source of carbohydrates, as is the case in social hymenopterans. Naive honeybees, which have never had contact with flowers, show distinct preferences for certain colours (Lunau et al. 1996; Briscoe and Chittka 2001). This ability might help newly hatched insects to find food.

Learning abilities in other parasitoids have been demonstrated both for host-related stimuli (Papaj and Vet 1990; Wäckers and Lewis 1994) and food-associated cues (Lewis and Takasu 1990; Takasu and Lewis 1996). Parasitoid food foraging may involve a broad range of possible sources (nectar, honeydew, host haemolymph, pollen, Bernstein and Jervis 2008) that should favour plasticity in response to food stimuli. Therefore, for parasitoids feeding on nectar,

both innate and acquired food preferences should be flexible to allow the use of a variety of flowering species. Associating clues detected at a distance to food resources would improve foraging efficiency and reduce the unpredictability of the environment. In this experiment, the innate preference for one colour did not prevent the individuals from associating the other colour with a food reward. This plasticity suggests that *V. canescens* would be a generalist food forager, as learning is expected to be more frequent in generalist species than in specialist parasitoids (Steidle and van Loon 2003). Studies on visual cues are scarce, especially in the context of food foraging. *Nasonia vitripennis* shows an increased preference for a colour rewarded with hosts or honey against an unrewarded colour (Oliai and King 2000). As shown by the same authors, males of the same species are able to learn to associate colours with the reward of virgin females. In this experiment, the parasitoids had to choose between the two different coloured halves of an arena. These animals could not display an intentional displacement towards a chosen target presented against a contrasting background. In Hymenoptera, colour contrast affects perception and could play an important role in the response of insects to coloured targets (Neumeyer 1980).

Schneider et al. (2002), have shown that irrespective of geographical location, thelytokous *V. canescens* populations form a relatively distinct genetical entity from arrhenotokous ones. In the experiments presented here, thelytokous and arrhenotokous wasps did not differ in their learning abilities during food foraging. This suggests that our results have a general scope for *V. canescens* although individuals of distant populations were not compared.

The innate preference for yellow may reflect an adaptation for flower foraging, as yellow is the most represented colour in natural flowers (30–40% of the flowering species of temperate regions, Weevers 1952; Kevan 1972). The preference for yellow may be the result of an adaptive response facilitating resource location, as shown in many flower foragers (Giurfa et al. 1995; Lunau and Maier 1995), or in the case of parasitoids, to select the most appropriate hosts, as shown in the egg parasitoid *Trichogramma ostriniae* (Lobdell et al. 2005). It has also been shown that the parasitoid *Cotesia rubecula* is innately attracted to yellow, and that this response depends on the hunger state of the individual (Wäckers 1994). In our experiments, *V. canescens* trained to associate yellow visual cues to food rewards did not enhance their preference of this colour when compared to control animals. This might be the result of limitations in the perception capacity of the animals. As reported by Gould (1993) and Menzel et al. (1993), for other Hymenoptera, the learning ability is higher for some wavelengths than for others. An alternative explanation is that a too strong preference for a given visual cue could be maladaptive in a changing environment as it could delay detecting

changes in the availability of different resources. This might be less critical for social bees, which rely on the foraging activity of the whole colony than for solitary nectar-feeders (Gould 1993). In this experiment, the preference for yellow rather than orange could be the consequence of a higher contrast of yellow against the background (white in our design) and a higher brightness. Contrast and colour are used as cues by food-foraging arthropods other than parasitoids. Examples are the crab spiders of the genus *Thomisus*, the sit-and-wait predators of honeybees that feed on nectar (Théry and Casas 2002; Théry et al. 2005).

Non-host-feeding parasitoids face a trade-off between two mutually exclusive activities: searching for host or searching for food. To decide how they should allocate time to each activity, these animals should integrate information on three key parameters: the probability of finding food (food availability), internal status (metabolic reserves) and host availability (Sirot and Bernstein 1996; Tenhumberg et al. 2006). Previous results show that *V. canescens* uses direct olfactory cues to estimate food availability (Desouhant et al. 2005; Lucchetta et al. 2007). This study suggests that these wasps could also use both innate and learned visual cues resulting from their foraging experience.

Despite the importance of food-searching activities in terms of fitness and the presence of numerous visual cues in natural conditions, very few studies have explored the learning of visual cues by parasitoids in this context (but see Oliai and King 2000). To our knowledge, this study is the first to show associative learning of visual cues in a parasitoid in the context of food searching in which the animal had to move intentionally towards the learned cue and had the alternative of not reacting to any cue. Future studies should address the ecological relevance of learning on visual cues in the field for this species.

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## Appendix

Colour locus in the colour space simulated for hymenopterans according to the Chittka (1992) model with spectral sensitivity functions of the standard photoreceptors for trichromatic Hymenoptera (adapted from Peitsch et al. 1992)

Table 1, 2, 3

**Table 1** Stimulations of the different photoreceptor types by each colour signal and the visual background

	Yellow	Orange	Blue	Background
Euv	0.1696	0.2455	0.3184	0.5
Eg	0.4719	0.3677	0.2290	0.5
Eb	0.1768	0.2071	0.3975	0.5

*Euv* stimulation of photoreceptors sensitive to ultraviolet, *Eg* stimulation of photoreceptors sensitive to green, *Eb* stimulation of photoreceptors sensitive to blue

**Table 2** Colour contrast between each visual stimulus and the background in the experimental conditions

Yellow	Orange	Blue
0.2988	0.1453	0.1461

**Table 3** Coordinates of each stimulus in the hexagon of colour vision of Hymenoptera

	Yellow	Orange	Blue	Background
x	0.2619	0.1059	−0.0774	0
y	−0.1439	−0.0995	0.1238	0

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