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What matters in the associative learning of visual cues in foraging parasitoid wasps: colour or brightness?

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Abstract Visual cues are known to be used by numerous animal taxa to gather information on quality and localisation of resources. Because environmental lighting can interfere with the spectral features of visual cues, the specific characteristics of the colour signals that promote forager decision and learning are still not known in the majority of insects (excepted in bees). We analysed the effect of previous experience on the use of visual information by the wasp *Venturia canescens*, a parasitoid of pyralidae, in the context of host searching. These parasitoids search for hosts concealed in several fruit species, so visual cues from the host microhabitat could play a key role in host finding. We also investigated the type of visual cues on which wasps based their decision. We tested whether wasps are able to associate an achromatic cue (brightness) or a chromatic one (hue, i.e. dominant wavelength and/or chroma) with the presence of hosts. Our results show that in the context of host foraging, chromatic cues are more reliable than brightness in achieving the associative

learning process. Therefore, understanding the behavioural ecology of foraging should make use of the knowledge about the visual information used.

Keywords Hymenoptera · *Venturia canescens* · Host foraging · Colour contrast · Brightness contrast · Cognitive ecology

Introduction

Visual cues or signals are involved in numerous decision-making processes in contexts such as foraging (Schmidt et al. 2004; Raine and Chittka 2007) or mate choice (Baeder and King 2004; Uy and Endler 2004), both in vertebrates and invertebrates. The use of this visual information is expected to reduce the uncertainty of the conditions in the environment and leads to adaptive behavioural responses to variability. Informative examples of evolutionary consequences of decisions based on visual cues are the co-evolution of plant–insect interactions (Shafir et al. 2003), speciation via mate choice (Gray and McKinnon 2007), and the evolution of display behaviour in mate choice (Endler and Théry 1996).

Detection and the use of colour cues might be influenced by the environmental context in which the colours are expressed. Indeed, the light spectrum that reaches the viewer's eye from a colour object depends on the ambient light spectrum reaching the object, the object's reflectance spectrum and the transmission spectrum of the environmental medium (Endler 1993). Consequently, the colour of an object can vary depending upon when and where it is viewed. For instance, in some insect pollinators, the light availability directly influences behaviours: plants in the sun receive more visits than plants in the shade, independently

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of the flower display size (Kilkenny and Galloway 2008). As light varies with time and location, the efficiency of communication and the reliability of cues vary as well. Reliability is crucial for foragers whose resources are associated with variably coloured microhabitats. Thus, insects pollinators and nectar foragers face the problem of identifying biologically relevant objects, like certain flowers, despite the very large variability of flower species and the changes that occur in illumination (Dyer 1998). Even if fitness can depend on the perception of visual cues in different lighting conditions, the specific features of the colour cue that promotes forager decisions and learning are less understood (except in bees, Horridge 2009, see discussion).

The use of a colour cue might also be dependent on its different physical features and on the sensitivity of the animals to these parameters. The colour of an object is a combination of chromatic cues, the dominant wavelength (hue) and chroma (saturation; Endler 1990), with the achromatic one, total brightness (total quantum flux in the spectrum integrated over the spectral range of the viewing animal). If two objects reflect equal numbers of photons but at different wavelengths, they could also appear to differ in brightness if the animal's sensitivity to light of different wavelengths is not the same (Hawryshyn 1982). In insects, colour cues are particularly important in honeybees and bumblebees, the most studied pollinators with respect to the relevance of colour vision for floral recognition (Chittka and Wells 2004). Bees have to adaptively choose between several plant species that differ in colour, shape, scent and temperature. Innate preferences help naïve bees find flowers on their first foraging trip away from the nest (Raine and Chittka 2007). Subsequently, as they gain foraging experience by visiting hundreds of flowers per day, they learn to associate floral traits such as colour, shape, scent and temperature with levels of reward (i.e. nectar but also warmth, Dyer et al. 2006). During the approach flight of honeybees, luminance contrast is perceived first, followed by colour contrast at a short distance (Giurfa et al. 1996). When foraging in an environment with several flower species, bees often make sequences of visits to flowers of the same colour independently of illumination conditions (the colour constancy mechanism, Neumeyer 1981) and then switch to another species. This indicates that the bees typically discount illumination in order to focus on a reliable cue, the hue (however, see Lotto and Chittka 2005).

In insect parasitoids, the use of colour cues also has behavioural relevance during the location of resources such as food (Lucchetta et al. 2008), hosts (Fisher et al. 2003) and mates (Oliai and King 2000). Non-host-feeding parasitoids often find their hosts and food in different locations, namely fruits for the hosts and generally flowers

for food (nectar). Associating colour cues with each kind of reward through a learning process should reduce the costs (in terms of time and energy) of searching for these resources and managing the trade-off between current and future fitness gains (Desouhant et al. 2005). However, learning a visual cue will be adaptive only if the cue remains reliable or constant whatever the environmental conditions. Consequently, this raises the question of the reliability of the colour features in natural environments. Should the animals learn hue, chroma or brightness? Despite their potential importance in host and food finding by parasitoids, few studies have been devoted to colour vision, i.e. the sensation of chromatic contrast independent of luminance contrast (Wardle 1990; Messing and Jang 1992; Fisher et al. 2003).

In this study, we aim to test whether the associative learning of the parasitic wasp *Venturia canescens*, which is able to associate a colour cue with a reward (Lucchetta et al. 2008), relies on chromatic (hue and/or chroma) or achromatic (brightness) cues. In orchards, *V. canescens* searches for hosts (mainly the pest *Ectomyelois ceratoniae* Zeller (Pyralidae)) that are concealed in fruits such as figs, carobs, dates, lemons and oranges. Because host microhabitats have the potential to provide colour cues for finding resources in the natural environments, we predicted that the associative learning of brightness should not be selected for because of the unreliability of this colour feature in variable environments.

Materials and methods

Venturia canescens (Hymenoptera: Ichneumonidae) is a non-host-feeding, solitary (only one offspring emerges per host), koinobiont (allows host development after parasitism) larval endoparasitoid of pyralid moths (Salt 1976) known to be a pest in granaries, mills and orchards. Because *V. canescens* is a generalist parasitoid, learning ability should be selected for (Geervliet et al. 1998). *V. canescens* parthenogenetic thelytokous females (i.e. that produce only female offspring) have been shown to be capable of associative learning in host- or food-searching activities: they are able to associate a volatile compound with a reward represented by an oviposition (Arthur 1971) and a coloured stimulus with a food source (Lucchetta et al. 2008). It attacks hosts in their second to fifth instar (Harvey and Thompson 1995). Host searching is elicited by a mandibular gland secretion (a kairomone) released by host larvae (Corbet 1971) when they feed. Kairomones are also used as volatile cues to localise host patches (Thorpe and Jones 1937; Castelo et al. 2003). While in a host patch, *V. canescens* searches for concealed hosts by probing the host kairomone-contaminated substrate with its ovipositor.

Ovipositions are recognised by a movement of the abdomen, the 'cocking' movement, by which *V. canescens* places a new egg in the tip of its ovipositor in preparation for the next oviposition (Rogers 1972). In at least 82% of the cases, a cocking movement is associated with an egg being deposited inside a host (Amat et al. 2003).

The wasps used in this study originated from Antibes (43.58°N, 7.12°E, France) and were collected in 2005 in the field. They were reared on the flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), which were fed on semolina and maintained in a constant environment at 25 ± 1°C and 75 ± 5% relative humidity under an artificial light–dark cycle (*L:D* = 12:12). The hosts originated from a mass-rearing facility located in Valbonne (Biotop), France. Experiments were performed in a controlled room (temperature 25 ± 1°C, 75 ± 5% RH) from between 10.00 and 17.00 h. 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.

Experiment 1: Learning association between chromatic cues and host patch

The aim of this experiment was to test the ability of *V. canescens* females to learn a colour cue characterised only by its chromatic features, dominant wavelength and/or chroma (used as the conditioned stimulus) associated to a host patch (the unconditioned stimulus). Females were first trained to choose between two colour stimuli differing in chromatic features but with the same perceived brightness (see below), where one stimulus was associated with a host patch reward (training sessions). Then, in a test session, females had to choose between the two colour stimuli in the absence of the reward.

The colour stimuli consisted of light-emitting diodes (LEDs). Because Lucchetta et al. (2008) showed that *V. canescens* is able to discriminate yellow and orange stimuli not independently of brightness, a yellow LED (BOSS, Type 34, diameter = 5 mm) and an orange LED (Kingbright, L-53SED, diameter = 5 mm) were chosen. Their peak wavelengths were 580 nm and 620 nm, and their half-band widths were 28 nm and 21 nm, respectively. The viewing angle was 60° for both LEDs. The brightness of both LEDs perceived by *Venturia* was 1.34 μmol/m^2 s (or 8.069 × 10^{17} photons/m^2 s). Since the spectral sensitivity of *Venturia* is unknown, calculations were based on the spectral sensitivities of honeybee photoreceptors (Peitsch et al. 1992), which are typical of many insects (Briscoe and Chittka 2001). The LEDs were positioned in 2 holes (12 mm diameter) drilled on the same side of a square Plexiglas box (165 mm × 165 mm × 95 mm, see also Lucchetta et al. 2008), at a 22 mm height from the bottom and 30 mm from the vertical left and right sides of the box.

The wasps used in the experiment were isolated at emergence between 8:00 and 10:00 h and kept in individual tubes (25 mm diameter × 75 mm height) with food (drop of 50% water-diluted honey) until 18:00 h of the emergence day. Tubes were kept in a controlled environment (25 ± 1°C, 75 ± 5% RH, *L:D* = 13:11) free of any host or food odours. The trials were carried out 24 h later in the experimental room.

In the training session, females were individually introduced into the Plexiglas box by a 5-mm-diameter hole in front of the LEDs. Two dishes were placed in the two corners opposite to the entrance (where the LEDs were positioned). One dish was a host patch, whereas the other one remained empty. Host patches consisted of 3-mm-deep 52-mm-diameter dishes containing host larvae and filled to the rim with clean semolina. We kept 12 *Ephestia kuehniella* larvae in the patch for 7 days before the experiment. The age of the host larvae was such that, by the seventh day, they had developed to the fifth instar. Both dishes were covered with a fine cloth to prevent larvae from escaping the host patch. When a wasp reached the host patch during training, it was allowed to probe until a cocking was observed. Each individual experienced three training trials spaced 2 h apart at 10:00, 12:00 and 14:00 h. Each experimental female was trained to associate yellow (*yellow training*) or orange (*orange training*) with a host patch reward. Control animals (*control training*) received a host patch reward at either LED.

Females were tested the same day as training at 16:00 h, at which time 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 10 consecutive seconds on one area of interest surrounding the LED corners. This area is constituted of 3 squares with 4-cm sides, drawn on the horizontal and the two vertical walls of the box near the two LED corners. If after 5 min of observation, a wasp did not make a choice, it was considered to be indecisive and was excluded from the statistical analysis. The locations of the two LEDs were reversed between training trials and between the last training trial and the test session. The Plexiglas box was washed after each trial. A same host patch was used three times by a female during its training session. The patches were replaced between the training and the test. A total of 72 animals were tested.

Experiment 2: Learning association between brightness and host patch

The goal of this experiment was to test whether when the wasps learn to associate a coloured cue with a reward they rely on an achromatic cue, brightness. To fulfil this goal, females were first trained to choose between two LEDs

differing in brightness (a bright and a dim one) but with the same chromatic features (hue and chroma), where one LED was associated with a host patch reward (training sessions). Then, in a test session, females had to choose between the two colour stimuli in the absence of the reward.

The same procedures as in Experiment 1 were used for training with a bright or a dim LED and the subsequent testing. The trials were conducted with the same box, room and conditions. The two orange LEDs used (same as in Experiment 1) had perceived intensities of 5.37 μmol/m^2 s (=3.234 $\times$ 10^{18} photons/m^2 s) for the brightest and 0.66 μmol/m^2 s (=3.974 $\times$ 10^{17} photons/m^2 s) for the dimmest. Their half-band widths were 21 nm. A total of 129 individuals were tested.

Spectral measurements

The photon flux rate emitted by the LEDs was measured with an Avantes AvaSpec-3648-SPU2 spectrometer calibrated in wavelengths between 232 and 797 nm and a FC-UV600-2-ME optic fibre connected to a CC3 cosine-corrected sensor. The spectrometer was calibrated in μmol/m^2 s using an Avalight-DH-Cal light source. Because bumblebees, which have a very similar spectral sensitivity as honeybees (Peitsch et al. 1992), use the stimulation of photoreceptors sensitive to green wavelengths to detect brightness contrast (Spaethe et al. 2001), we used the spectral sensitivity function of this photoreceptor type (Peitsch et al. 1992) to measure the brightness of the LEDs perceived by *V. canescens* wasps. Because spectral sensitivity curves are not available for *V. canescens*, we used the spectral sensitivity functions of the photoreceptors of honeybees *Apis mellifera* (Peitsch et al. 1992). The used lambda max values (photoreceptor peak sensitivities) are those of the honeybee's three photoreceptors types, as determined by Peitsch et al. (1992): UV = 344 nm, blue = 436 nm, green = 544 nm.

A variable resistance associated to each LED was used to obtain the adequate intensity for each experiment. Brightness (achromatic) and colour (chromatic) contrasts between LEDs were computed using the physiological model of Vorobyev and Osorio (1998), also presented in Kelber et al. (2003). The model is computed with neural noise only, as in Håstad et al. (2005). The weber fraction is 0.13. Colour contrast values of less than 1 just noticeable difference (jnd) indicate that the difference between two stimuli is indistinguishable, while values >1 jnd indicate that the difference between two stimuli can be detected. The colour contrast was high in Experiment 1 and not detectable in Experiment 2, while the reverse was true for brightness contrast (Table 1). To determine whether the stimuli used in Experiment 1 differ in hue and/or chroma, we plotted the LED spectra in the colour space of

honeybees (Chittka 1992), using the fluorescent light and the white background present in the experimental room. Both yellow and orange LEDs had very similar coordinates in that colour space (yellow: $x = 0.854$, $y = -0.492$; orange: $x = 0.856$, $y = -0.493$). This apparently shows that both stimuli have the very similar hue and chroma when using honeybees' spectral sensitivities. However, the use of the model of Vorobyev and Osorio (1998) does not allow the identification of which chromatic feature, either perceived hue or chroma, generates the chromatic contrast between LEDs (and not between each LED and the background) in Experiment 1. We also measured quantum catches for the UV-, blue- and green photoreceptors viewing the LEDs used in both experiments (Table 2).

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 the learned coloured stimulus: the yellow and the brightest LEDs in Experiments 1 and 2 (target LEDs), respectively. The explanatory variables were the position of the coloured stimuli (two modalities: left or right, Experiments 1 and 2) and the conditions of training (three modalities: yellow, orange and control in experiment 1; bright LED, dim LED and control in Experiment 2), including the position of the target LEDs during the test session. Statistical analyses were performed using R software (R Development Core Team 2008).

Table 1 Visual contrasts between the LEDs used in the two experiments, computed with the physiological model of Vorobyev and Osorio (1998)

	Brightness contrast	Colour contrast
Experiment 1	0.046	5.147
Experiment 2	6.973	0.743

Values are jnds (just noticeable differences)

Table 2 Photon catches (in μmol/m^2 s) of the three photoreceptor types upon viewing each LED used in the experiments

	UV	Blue	Green
Experiment 1			
Yellow	0	0.0007	1.3362
Orange	0	0.0002	1.3178
Experiment 2			
Bright orange	0	0.0007	5.3179
Dim orange	0	0.00008	0.6595

Results

Learning association between chromatic cues and host patch

Venturia canescens clearly shows the ability to learn a colour characterised only by its chromatic cues and associated with a host patch reward. When females were conditioned to find a host patch associated with an orange stimulus (*orange training*), they preferentially chose this colour in the test session (16 out of 25 wasps, 64%), while 34.8% (8 out of 23) of the females in the *control training* group (i.e. conditioned with host patch associated with both wavelengths) were attracted by this colour (Fig. 1). The difference in preference for orange between the two training conditions is significant (contrast *orange training* versus *control training*: z-value $= -1.99$, $P = 0.04$). Out of 24 females conditioned to yellow (*yellow training*), 14 (58.3%) 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 (contrast *yellow training* vs. *control training*: z-value $= -0.48$, $P = 0.63$) and reflects the innate preference (65.2%) 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 (contrast *orange training* versus *yellow training*: z-value $= -2.05$, $P = 0.04$; Fig. 1).

Learning association between brightness and host patch

Whatever the brightness of the LED the females were trained on, they did not show any preference. In the *control*
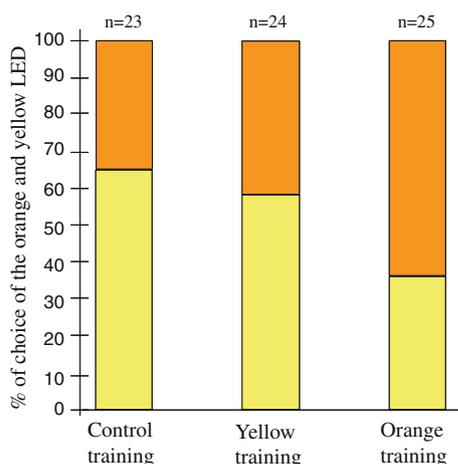

Fig. 1 Conditioned colour choice with host patch reward: mean proportion of *yellow* or *orange* LED choice during the final test according to the learning conditions (host patch associated with *yellow*, *orange* or *both* LEDs in the control training). *n* Represents the number of wasps tested
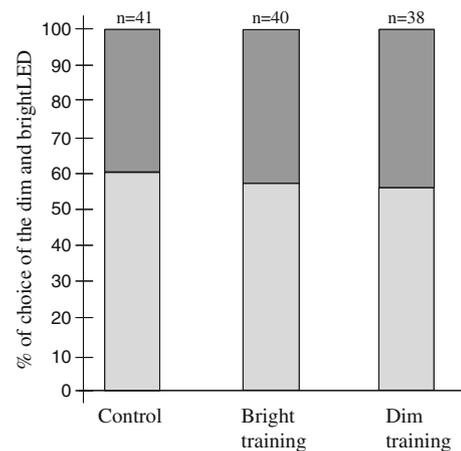

Fig. 2 Conditioned brightness choice with host patch reward: mean proportion of *dim* or *bright orange* LED choice during the final test according to the learning conditions (host patch associated with *dim*, *bright* or *both orange* LEDs in the control training). *n* Represents the number of wasps tested

training group (i.e. those conditioned with a host patch associated with both brightness values), 56.1% of females (23 out of 41) were attracted by the brightest LED (Fig. 2). This percentage is not significantly different from a random choice (intercept: z-value $= 0.78$, $P = 0.44$; Fig 2). A total of 60.5% of the wasps (23 out of 38) conditioned to find the host patch associated with the dimmest LED orange (*dim training*) chose the brightest in the test session. The difference in preference between the two training conditions is not significant (contrast *dim training* versus *control training*: z-value $= 0.40$, $P = 0.69$). Out of 40 females conditioned to the brightest LED (*bright training*), 23 (57.5%) chose the learned LED in the test session (contrast *bright training* versus *control training*: z-value $= 0.13$, $P = 0.90$).

During the first trial of the training session, there was no innate preference for the brightest LED. Of the 41 wasps, 58.53% chose the brightest LED (intercept: z-value $= 0.34$, $P = 0.28$).

Discussion

Our results show that visual cues can be involved in host searching in the parasitoid *V. canescens*. When a colour cue is rewarded with ovipositions, then this chromatic cue becomes reliable information for host searching. The main originality of our study lies in the fact that we show that different features of a colour stimulus do not have the same informative value and/or might not be used in an associative learning process. Thus, *V. canescens* females respond to the chromatic feature of the colour stimulus and not to its brightness: they associate the chromatic cue to a reward

in a learning process. Our results raise questions on the adaptive significance of the differential responses to the features of colour cues for host searching in natural conditions, as well as on the cognitive processes and spectral sensitivity of parasitoids.

In our study, *V. canescens* females are able to associate the orange-coloured stimulus with a reward (oviposition) in a learning process. This corroborates previous results showing associative learning between a colour cue and food reward (Lucchetta et al. 2008), but in this early study the brightness was not controlled for. In either work, *V. canescens* trained to associate yellow visual cues to host rewards did not enhance their preference of this colour when compared to control animals. Yellow is a strong innately preferred colour in *V. canescens* over orange and blue (Lucchetta et al. 2008), which could explain why the preference is not enhanced after training with this colour. This could also be explained by the fact that for other Hymenoptera, the learning ability is higher for some wavelengths than for others (Gould 1993; Menzel et al. 1993). An alternative explanation is that too strong of a preference for a given visual cue could be maladaptive in a changing environment as it could delay the detection of 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).

The ability of associative learning between visual cues and the host was expected in this species. Indeed, *V. canescens* is a generalist parasitoid that parasitises several host species (Salt 1976) in a broad range of microhabitats (fruits such as carobs, almonds, lemons, oranges, figs) in which numerous colour cues are present. This should favour plasticity in response to stimuli associated with host presence. Moreover, the potential host microhabitats (i.e. fruits) are variable from generation to generation but are relatively constant within a generation. Females have then the ability of finding hosts associated with the same microhabitat in consecutive searching bouts. In other insects, and particularly in parasitoids, associative learning has been well documented for host related stimuli (Papaj and Vet 1990; Papaj and Lewis 1993). However, most studies focused on associative learning between olfactory cues and a reward. Our study contributes to filling this gap.

Why could it be relevant to learn a chromatic cue rather than brightness when foraging for hosts in a natural context? First, colour is a relatively stable cue. The reflectance of green foliage is quite consistent over a wide range of plant species. Due to receptor adaptation and to the equally intense reflection of foliage in all regions of the insect's colour spectrum, insects perceive foliage as mostly grey. Against this achromatic background, any wavelength composition other than that of foliage will produce at least some colour contrast (Chittka et al. 1994). Colour detection is less dependent on a precise visual recognition than is pattern resolution (Land 1997). This means that parasitoids that use visual cues for their orientation could detect colour stimuli from a longer distance, whereas information about the specific shape of the plants and patterns of damage would be mainly available at closer range. Second, the learning of a host microhabitat hue may allow parasitoids to identify plant structures (e.g. leaf or fruit) that their foraging experience has revealed as a profitable resource. This should give an adaptive advantage by reducing the time wasted on the decision of where to search for hosts. According to optimal foraging theory, search time is a key parameter defining the profitability of the resource (Stephens and Krebs 1986). Once a host population (a tree or a group of trees with fruits) is reached, *V. canescens* females could use the learned cues to increase their efficiency for a precise localisation of the hosts. The use of visual cues does not preclude the well-known use of olfactory cues to select host microhabitats. For instance, ambrosia beetles integrate both odours from hosts and visual cues not related to the host plant in order to select host plants (Campbell and Borden 2009). The results of Experiment 1 show that wasps can discriminate between yellow and orange stimuli of high chromatic contrast but low achromatic contrast. This is surprising because these stimuli have the same colour and hue in the colour space of honeybees. Furthermore, it differs from results of von Helversen (1972): yellow and orange are not distinguishable by hue in the colour space of bees. However, Chittka and Waser (1997) showed that bumblebees were able to discriminate yellow and orange step reflectance functions. How and whether this discrimination is independent of intensity is still an open question. Because our conclusions are drawn from the model of Vorobyev and Osorio (1998) developed for *Apis mellifera*, *V. canescens* may have different photoreceptor characteristics and colour discrimination abilities than honeybees. This calls for a specific study of colour vision in *V. canescens* to determine the spectral sensitivity functions of this species and which particular spectral reflectance functions are used.

Why did not *V. canescens* rely on brightness in the associative learning process? Note that this non-significant result does not seem to be the consequence of a lack of statistical power: we were able to show the ability of *V. canescens* to learn coloured stimulus with a smaller sample size. Two explanations can be put forward to explain the absence of response after training stimuli of different brightnesses. First, the wasps are not sensitive to the brightness of a cue. However, the ability to respond to brightness is present in other hymenopterans. Bees change their behaviour in response to brightness in a phototaxis context. Conversely, the parasitoid *Exeristes robator* could

not be trained to distinguish between two grey stimuli that strongly differed in brightness (Wardle 1990). At a large spatial scale, when dispersing between host populations, i.e. when selecting a host habitat, *V. canescens* females are sensitive to illumination. They avoid sunny areas and prefer shady areas with relatively high vegetation density (Desouhant et al. 2003). Bumble bees can also perceive spectral changes in illumination conditions, even in the context of a task that does not require colour processing (Dyer 2006). The second hypothesis is that individuals do not use brightness as a cue in the learning and decision-making processes because of its unreliability under variable environmental conditions, which can be, to some extent, compensated for by photoreceptor adaptation and colour constancy. We favour the last hypothesis and some results tend to support it. Other works have inferred from their own results that colour learning is also based on hue learning (Messing and Jang 1992; Oliai and King 2000; Traynier 1984), but did not include control assays. Wäckers and Lewis (1999) conditioned *Microplitis croceipes* to distinguish between two colours of approximately the same brightness. In the context of microhabitat selection, a single study in parasitoids has shown, in conditions of controlled brightness, that *Exeristes robator* was able to discriminate between two different hues based on actual colour learning and not on brightness (Wardle 1990).

If rarely described in parasitoids (see also Segura et al. 2007) in habitat selection context, the use of chromatic cues rather than brightness has been described in wasps (Shafir 1996) and bees (Chittka et al. 1992). In honeybees, it is known that brightness differences play no role in a discrimination task, for as long as colour cues are available (Backhaus 1991). It is much more difficult to train bees to respond to differences in brightness than in hue (von Helversen 1972; Backhaus and Menzel 1987; Chittka 1999). Models of colour vision in bees are all two-dimensional and do not include a brightness dimension (Vorobyev and Brandt 1997), although extensively trained bees can learn to use signal brightness to discriminate stimuli (Menzel and Backhaus 1991).

The ability to use of brightness or chromatic cues as informative cue might be species- and context-dependent and could explain the interspecific variability in this ability. Environmental pressures may have selected for different hue or brightness sensitivities. In *Apis mellifera*, Giurfa and Vorobyev (1998) showed that, in the context of target detection, the achromatic contrast channel specialises in the detection of objects of reduced angular size, whilst the chromatic channels are specialised for objects of large angular size. They suggested that achromatic detectors with a centre-surround organisation are involved in the task of detecting achromatic targets. Hue and brightness are not used at the same distance. The common bee would use

brightness contrast between 5.7 and 1.9 cm to detect our colour target (LED 5 mm in diameter) and colour contrast below 1.9 cm. In our experiments, we did not record the searching behaviour of targets once the wasps entered the experimental enclosure. However, they do not directly move towards the chosen LED (E. Desouhant Pers. Obs.).

Our results contribute to filling the gap in our knowledge about the visual cues used in the target identification of non-bee species. Our study and other examples from the foraging literature attest a general need to consider how colour features might be tuned to details of host–parasitoid interactions, not only in terms of sensory and cognitive profiles of the parasitoid but also in the contexts where the encounters occur. Our results also suggest that understanding the behavioural ecology of foraging can benefit from knowledge about the visual information used.

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