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ORIGINAL PAPER

The interaction of temperature and sucrose concentration on foraging preferences in bumblebees

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Abstract Several authors have found that flowers that are warmer than their surrounding environment have an advantage in attracting pollinators. Bumblebees will forage preferentially on warmer flowers, even if equal nutritional reward is available in cooler flowers. This raises the question of whether warmth and sucrose concentration are processed independently by bees, or whether sweetness detectors respond to higher sugar concentration as well as higher temperature. We find that bumblebees can use *lower* temperature as a cue to *higher* sucrose reward, showing that bees appear to process the two parameters strictly independently. Moreover, we demonstrate that sucrose concentration takes precedence over warmth, so that when there is a difference in sucrose concentration, bees will typically choose the sweeter feeder, even if the less sweet feeder is several degrees warmer.

Keywords Pollination · Sensory ecology · Sensory integration · Sweetness detection

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Introduction

Many flowering plants rely on insect pollinators for reproductive success and employ a dazzling array of tactics to attract and retain their services. Nutritional rewards, such as pollen and nectar, are advertised by features such as flower size, scent and colour. The rewards offered by flowers to pollinators can be as diverse as the methods of advertisement used. Shelter, in the form of a brood site (as in the case of the fig and fig–wasp interaction (Grandi 1961)), an overnight abode (for example *Philodendron* and *Oncocyclus* flowers (Sapir et al. 2006; Seymour et al. 2003)), or a temporary resting or basking place can all be a reward for pollinators. A floral temperature that is above ambient temperature can also act as a reward and can increase the number of pollinator visits to a flower (Herrera 1995; Kevan 1975; Sapir et al. 2006; Seymour et al. 2003). Many pollinators are ectotherms, and are therefore sensitive to fluctuations in environmental conditions. While some insect species, such as bumble bees (*Bombus* spp.) are able to control their body temperature and so gain a certain degree of freedom from environmental conditions, this independence comes at a metabolic cost, as significant amounts of energy are required to maintain body temperature (Heinrich and Esch 1994; Bishop and Armbruster 1999). Previous work has indicated that warmth alone can act as a metabolic reward for pollinators, and beetle and fly pollinators may actively seek out warm flowers, even if they lack any nutritional reward (Sapir et al. 2006; Seymour et al. 2003). However, floral temperature could also influence pollinator behaviour in other ways. In a range of plant species, warmer flowers produce more nectar of higher sugar concentration than that produced by cooler flowers, perhaps through increased evaporation (Corbet 1978). Therefore, floral temperature could also be used as a cue to help determine nectar quality. Temperature could also act as a "dishonest" signal; if the sucrose receptors of pollinators are unbuffered against temperature and temperature directly modulates the transduction of the sweet taste, as is the case for humans (Bartoshuk et al. 1982; Talavera et al. 2005), temperature could act to confound the sucrose perception of the pollinator. An increased stimulation of pollinator sucrose receptors at higher temperatures would allow warmer flowers to simulate higher sucrose concentrations than colder flowers, despite both flowers possessing equal nectar quantities and qualities.

We are interested in how particular floral traits function in pollinator attraction, and here explore whether temperature can function as an advertisement or cue independently of the role of warmth as a metabolic reward. In this context, a reward is defined as an advantageous compensation that positively enforces a specific behaviour, while a cue has been defined as an incidental feature present in the environment that has not been selected to carry specific meaning for intended receivers (Saleh et al. 2007; Seeley 1995).

In this paper, we address the following specific questions:

(1) Can bumble bees (*Bombus terrestris* L.) use temperature as a cue independently from any heat-based metabolic reward or any innate preference for warmth?
(2) How does bumblebee preference for warmer nectar interact with preference for sweeter nectar, and can such preferences allow us to discriminate between heat as a metabolic reward and as a false sweetness signal?

Materials and methods

All experiments were carried out using *B. terrestris* colonies (Koppert Biological Systems) housed in a plastic nest box connected to a flight arena (110 cm L, 70 cm W, 100 cm H) by means of a transparent pipe, regulated by a series of gates. Pollen was fed directly into the nest. One colony of bees was used per experiment. These bees had never foraged from natural flowers and were naïve with respect to the experimental setup before training began. Coloured paints were used to mark individual foragers and each individual was used only once for each experiment. The room temperature was measured on a twice daily basis (19.5°C±0.1°C S.E., n=30). The temperature of the room, gravity feeders and artificial flowers was measured with a Hanna (Cluj-Napoca, Romania) HI 8757 portable microprocessor K-type thermocouple. To increase the sensitivity of the thermocouple, a short piece of thinner (0.05 mm) wire (made of the same metal alloy as the thick wire i.e. one of chromel, the other of alumel) was soldered onto the thicker wire (Wires, all from RS Components Ltd Corby, UK) using a standard aluminium solder. The wires were then insulated using a spray-on electrical circuit lacquer (Comba et al. 2000). Illumination was provided by six Sylvania Activa 172 Professional 36W fluorescent tubes (Germany) that were modified with Phillips high frequency ballasts to have a flicker frequency greater than 1,200 Hz on a 12-h light/dark regime.

Control—to test whether bees could discriminate quinine and sucrose solutions by means other than contact chemoreception

Experiment 1 below hinges critically on bees' inability to identify rewarding feeders (containing sucrose solution) and alternative feeders (containing bitter quinine hemisulfate solution) before they have tasted these feeders' contents. Quinine and sucrose are traditionally thought to be odourless tastants, but there is some evidence indicating that some human subjects can detect their solutions by scent (Mojet et al. 2005). Honeybees have previously been shown not be able to discriminate such feeders by smell (Dyer and Neumeyer 2005), but a direct proof for bumblebees remains outstanding. In addition, quinine fluoresces under UV light (Pye, in press) and although such fluorescence effects are often invisible under daylight conditions (Kevan 1976), we preferred to test directly whether quinine-filled feeders could be discriminated from sucrose solution feeders by bumblebees before landing. To this end, ten artificial flowers (blue plastic disks; ∅= 26 mm, 4 mm thick; Dyer and Chittka 2004) with a hole in the centre to hold fluid (∅=4 mm; depth 2.5 mm) were placed in the arena at spatially randomised coordinates. Five stimuli were rewarded with 20 µl of 50% (vol.) sucrose solution, and the other five visually identical stimuli contained 20 µl of 0.012% (saturated) quinine hemisulphate salt solution in water. Five individual bees were allowed to make 100 flower visits each, which typically took several foraging bouts (round trips from the nest to the flowers and back); between bouts, all flowers were cleaned with ethanol and replaced with fresh ones.

Experiment 1—to test the putative role of temperature as a cue independent of its role as a reward

To test whether temperature can act as a cue independently of a metabolic reward or any innate preference for warmth, artificial flowers were constructed from Sterilin tubes (Bibby Sterilin Ltd., Stones, Staffordshire, UK) (diameter= 26 mm; height=8 cm). The inverted lid of a 0.5 ml Eppendorf tube (Hamburg, Germany) was attached to the top of each artificial flower (See Fig. 1a). Ten visually identical artificial flowers were presented to each individual bee. Whilst visually identical, the flowers differed in temperature; the five 'warm' flowers were 8.7 (±0.3°C S.E., n=20) warmer than the other five flowers, which were at room temperature. The temperature 0.5 cm above the top of the 'warm' flowers was also recorded and found to be 3.7°C above room temperature (±0.2°C S.E., n=20). The temperature difference of the flowers was maintained by filling the Sterilin tube under each flower with water at the required temperature. These flowers were frequently exchanged with flowers kept in a warm or cool water bath and the temperature of flowers monitored on removal, to ensure no significant changes had occurred during the experiment. The warm flowers were replaced with freshly warmed ones from the water bath after 10 mins or two bouts, whichever was shorter.

Bees visiting cool flowers were rewarded with 20 µl of 30% (vol.) sucrose solution placed within the Eppendorf lid, and bees visiting warm flowers were penalised with 0.012% quinine solution (Chittka et al. 2003). The flowers with sucrose were replenished immediately if the contents of the flower were drunk, once the bee had departed. After each bout of visits by an individual bee, all "flowers" were replaced with flowers that had been cleaned with 30% ethanol to remove any scent marks, and had been in the requisite water bath long enough to return them to the correct temperature. Starting at the first contact of each bee with the two flower types, the choices made by each of ten individual bees for 100 landing events were recorded. A correct choice was scored as the bee landing on a warm flower but *not* drinking, or landing on a cool flower and drinking. An incorrect choice was scored as the bee landing on a warm flower and drinking, or landing on a cool flower and *not* drinking.

Experiment 2—to investigate the interaction between warmth and pollinator perception of sweetness

To investigate the extent to which perception of sweetness and direct metabolic reward may each influence bee preference for warmer flowers, the bees were presented with gravity feeders of the sort described by von Frisch (1967). Two visually identical feeders (A and B) were used (see Fig. 1b), both of which were placed on DB-2A heating blocks (Techne, Cambridge, UK). The block around the gravity feeder was insulated with 7 mm of polystyrene, so only the sucrose inside the feeder was heated (Dyer et al. 2006). The temperature of the sucrose was checked at hourly intervals to ensure accurate heating and thorough mixing. The feeders were of equal distance from the entrance to the colony, but on opposite sides of the flight arena. Feeder A was always at room temperature, but over the course of the experiment contained a series of sucrose concentrations (30%, 25%, 23% or 21.5%, v/v). Feeder B always contained 20% sucrose, but differed in temperature throughout the experiment (either room temperature, or 8°C above room temperature). A series of comparisons was carried out, comparing bee preference for each concentration of sucrose in feeder A to that of 20% sucrose at either room temperature (19.5°C±0.1°C S.E., n=30) or 8°C above room temperature in feeder B (7.8°C±0.2°C S.E., n=30). For each comparison, all foraging bees were allowed access to the gravity feeders for 1 h before data collection began, so that they were familiar with the experimental set up. The number of foragers visiting each feeder was recorded for 1 h, after which the gravity feeders were cleaned with ethanol and the sides of the arena at which the two feeders were placed were switched to control for directional preferences. For each set of variables, four data sets were collected, giving 32 sets of observations in total, and the order of presentation was randomised to control for accumulative learning by the bees.

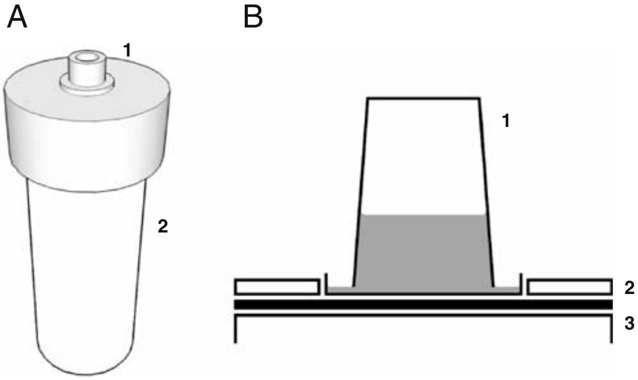

Fig. 1 **a** Setup for experiment 1. An Eppendorf lid (*1*) was attached to the lid of a water-filled Sterilin tube (*2*; height 8 cm). **b**. Setup for experiment 2. A gravity feeder (*1*) was placed on a foil-lined heating block (*3*). The area of the heating block around the gravity feeder was insulated with a sheet of polystyrene (*2*). The height of the heating block is 10.5 cm, and the feeder's height is 12 cm. Not drawn to scale

The proportion of visits made to the cold feeder was calculated for each bout. The mean proportion of visits was calculated for each of the sixteen combinations of sweetness, warming and feeder positioning (where two replicates were conducted for each of these combinations) and a three-way analysis of variance (ANOVA) (including interaction terms) was conducted on these values (which were arcsine transformed to ensure that statistical assumptions of normality were followed).

Results

Control—to test whether bees could discriminate quinine and sucrose solutions by means other than contact chemoreception

Figure 2 (black bars) clearly indicates that bees' olfactory system could not discriminate between artificial flowers on the basis of the solution (sucrose or quinine) that these contained, prior to actually landing on a flower. When temperature was provided as a cue, bees quickly learnt to avoid the quinine-containing flowers (see Fig. 2 white bars and section below), but even over 100 trials no learning

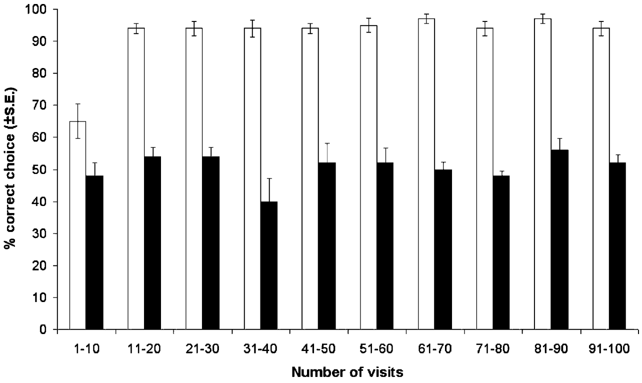

Fig. 2 Percentage of correct choices made by ten bumblebees over 100 visits each as a function of trial number, using temperature as a cue to distinguish between room temperature (correct) and an 8°C warmer (incorrect) flowers (*white bars*). *Black bars* indicate percentage of correct choices of bees choosing between artificial flowers where one type contained sucrose solution and the other quinine. Bees showed no indication of mastering this task even after 100 trials

was apparent when no temperature cue was provided. At the end of the experiment (last 20 flower visits in each bee) the percentage of correct choices was still only 54%. When pooled, these decisions are non-significantly different from chance (χ^2=0.18; df=1; p=0.67).

Experiment 1—to test the putative role of temperature as a cue independent of its role as a reward

Bees were unable to judge the temperature of the feeders while they were still in flight, either by IR perception or by temperature sensing. The number of landings on the warm or cool feeders did not differ significantly from that expected by chance (number of landings each bee made to a warm flower in 100 visits=49.3±0.75 S.E., t_9=0.93, p=0.37), and there was no change seen in visits over the course of the observations (number of visits to warm flowers in first ten landings: 5.1±0.31 S.E., number of visits during last ten landings: 4.8±0.29; paired-sample t_9= 0.63, p=0.541). However, *after* landing, all ten tested individuals were able to use temperature as a cue to locate and drink from the cooler rewarding feeder (and to avoid drinking from the warm feeder). Figure 2 shows the mean learning curve for the ten bees. Within the first ten visits, the bees already improved to an average of 65% correct choices (t_9=2.76, p=0.022). After 20 visits, bee choices were correct almost 100% of the time (average mean 94% correct, ±1.63 S.E.; this constitutes a significant improvement over the first ten choices: paired-sample t_9=4.94, $p<$ 0.001), and performance saturated at this point. It is thus clear that temperature can be used as a cue to solve a task independently of any metabolic reward, and that this temperature perception is not occurring through proboscis-based receptors since the choice is made before proboscis extension (but after landing).

Experiment 2—to investigate the interaction between warmth and pollinator perception of sweetness

The proportion of bee visits to the sweeter feeder (feeder A) increased significantly with increasing sucrose concentration when both feeders were at room temperature ($F_{3,3}$= 72.7, p=0.003, Fig. 3). For example when the sweeter feeder contained 30% sucrose, as compared to the less-sweet feeder's 20% sucrose, 88% of bee visits occurred at the sweeter feeder. However, there was no effect of warming on the proportion of bee visits to the less sweet feeder ($F_{1,3}$=3.9, p=0.143).

The position of the feeders in the flight arena were also found to significantly affect the proportion of visits ($F_{1,3}$= 29.9, p=0.012), indicating that there was a site preference; thus to exclude that this site preference produced the observed response to sweetness, we also included interaction terms in the ANOVA. Neither of the position interactions were significant (warming×position: $F_{1,3}$= 1.02, p=0.387; sweetness×position: $F_{3,3}$=0.26, p=0.849). Inspection of Fig. 3 suggests that at the lowest sweetness difference, the bees may prefer the warmer feeder, but post hoc tests suggest that this difference is not significant (Tukey HSD comparing the two data points: p=0.594). The results of the ANOVA model confirms this, in that the interaction between warming and sweetness was not significant ($F_{3,3}$=5.74, p=0.092).

Discussion

Our first experiment showed that bees could use warmth purely as a cue—and one that they could associate with negative stimuli. This allows us to conclude that bees can use temperature as a cue independently of a metabolic reward. It also shows that they can learn to use temperature

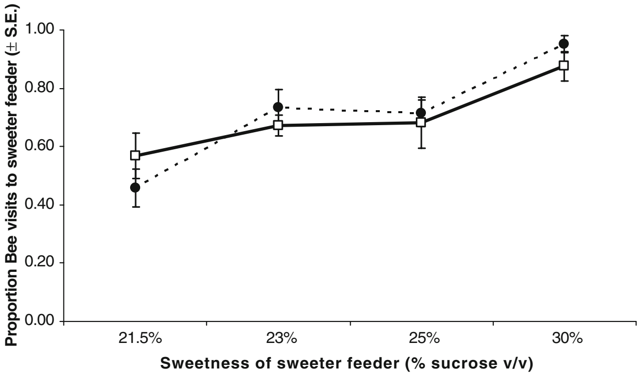

Fig. 3 Proportion of bee visits to the sweeter feeder at different sucrose concentrations when both feeders were at room temperature (*unfilled squares with solid line*) and when the less sweet feeder was warmed by 8°C (*filled circles with dotted line*). The *error bars* indicate the standard error

as a cue independently of a preference for warmth. This experiment also indicates that bees can distinguish flower temperature without using proboscis-based receptors of viscosity, concentration or temperature. As sucrose was only present in one of the two types of artificial flowers, and the bees were still capable of distinguishing between them, factors other than nectar viscosity can help the bee to determine the state of the floral environment. Since choices were made after landing but before drinking, we conclude that antennae or tarsal receptors were used to detect floral temperature. Indeed, Heran (1952) showed that most temperature sensors in honeybees are located on the antennae, although some individuals whose antennae had been removed still showed marked temperature preferences, from which he concluded that there might be temperature receptors also in other body areas, for example the proboscis. Heran (1952) also showed that bees could distinguish differences of only two degrees in room air temperature, indicating that the bees in our experiment might in theory have access to feeder temperature before landing (since air temperature 5 mm above the warmer feeder was 3.7°C above ambient temperature)—but rejections in our tests were made only after landing, and so perhaps the time spent traversing the limited space with elevated temperature was too short for the bees to notice the difference.

While increased floral temperature can act as a direct metabolic reward (Seymour et al. 2003), it is also possible that it acts as a “trick” to convince pollinators that the available nectar is richer in sucrose than it really is. It is unknown whether the sucrose receptors of bumblebees are buffered against temperature variation. If they are not (as in humans; Bartoshuk et al. 1982; Talavera et al. 2005), a variation in temperature might confound the sucrose perception of the pollinator. For example, Lacher (1964) found that the firing frequency of honeybees’ antennal CO_2 receptors increases with temperature, while that of antennal scent receptors decreases at higher temperatures. A further complication for heat-unbuffered receptors might arise because body temperature changes with the concentration of sucrose solution that a bumblebee imbibes (Nieh et al. 2006). Our results, however, indicate that sucrose concentration and temperature are processed independently and hierarchically, where sucrose concentration takes priority. Only when the difference in sucrose concentration was low, and the less concentrated feeder was substantially warmer, bees appeared to slightly prefer the warmer feeder (Fig. 3)—but this difference was not significant, and statistical analysis did not reveal an effect of warming on feeder preference when two feeders differed in sucrose concentration. Such hierarchical processing when distinct sensory cues are in conflict has been observed in several behavioural contexts, for example the use of landmarks versus celestial cues in navigation (Menzel et al. 1990; Chittka and Geiger 1995). Perhaps unsurprisingly, experiment 2 indicated that an increase in the sucrose concentration led to an increase in the proportion of visits to the sweeter feeder relative to the less sweet feeder, as in other insects (Blüthgen and Fiedler 2004, Schmidt et al. 2006, Stromberg and Johnsen 1990, von Frisch 1967).

Viscosity of reward could be another factor affecting bee preference. Both temperature and sucrose concentration affect viscosity; an increase in sucrose concentration increases the viscosity, while an increase in temperature decreases it. However, ingestion rates for bumblebees imbibing sucrose solution are unaffected by concentrations from 10–40% and their corresponding viscosities of $1<\mathrm{cp}<7$ (Harder 1986). As no sucrose solution over 30% was used, even with the increase in temperature all of the scenarios described in this paper fall within this viscosity window (Génotelle 1978); thus viscosity is unlikely to have affected our results.

The use of temperature as a cue may be of significance both to pollinators and to plants. A link between floral temperature and the production of a higher quantity and quality of nectar has been found (Corbet 1978), and models have shown that a heat reward is an economically feasible reward for a plant to offer pollinators in return for their services (Rands and Whitney 2008).

Pollinators therefore stand to benefit from increased quantity and quality of nectar if they can use cues to identify the warmest flowers. Temperature is also thought to influence the rate of pollen development (Kevan 1989), suggesting that warmer flower would also be a better source of larval nutrition. Different cellular structure in the floral surface also appears to influence floral temperature (Comba et al. 2000), which may have importance for why bees prefer warmer flowers when cooler flowers contain identical concentration sucrose solution (Dyer et al. 2006).

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