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Preferences and tradeoffs in nectar temperature and nectar concentration in the Asian hive bee *Apis cerana*

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Abstract Honey bee foragers need to asses and make trade-offs between a number of potentially conflicting floral attributes. Here, we investigate multi-attribute decision making in the eastern honey bee, *Apis cerana*, when foraging on food sources that varied in warmth and sucrose concentration. We show that foragers prefer warm (30 °C) sucrose solution over cool (10 °C) sucrose solution and concentrated (30 % w/w) sucrose solution over dilute (15 % w/w) sucrose solution. When we offered the preferred sucrose concentration (30 % w/w) at the less-preferred temperature (10 °C), and the less-preferred sucrose concentration (15 % w/w) at the preferred temperature (30 °C), foragers prioritized warmth by choosing the warmer, but lower concentration solution. When the temperature difference was less extreme, bees preferred more concentrated cooler syrup (30 % ww at 15 °C over 15 % 30 °C). However, the addition of a decoy item to the choice set had a significant effect on the bees' preferences. Our results highlight the critical importance of considering context effects when measuring the foraging preferences of animals.

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Introduction

Animals are often faced with choices about what and where to eat, who to mate with and where to nest. Each alternative may be described by an array of attributes, some or all of which the animal may need to take into account before making a decision. Animals foraging for food might simultaneously consider the caloric value of a food, the effort and handling time required to access the food (Shafir 1994), the risk of predation (Dukas 2001; Brown and Kotler 2004; Abbott and Dukas 2009), microclimate in the food patch (Webster and Dill 2006; Latty and Beekman 2010), the presence of toxins in the food (McArthur et al. 2012; Tan et al. 2012a), and the balance of protein and carbohydrates in a food (Simpson et al. 2004). Decision-making can be complicated when two or more attributes are in conflict, so that the animal must balance opposing criteria. For example, the tendency of high-quality food patches to attract predators means that foragers may have to make trade-offs between patch quality and the risk of predation (reviewed by Brown and Kotler 2004). Since many (if not all) foraging decisions can be characterised as being multi-attribute, understanding how animals deal with multiple, sometimes conflicting, attributes is a key issue in foraging ecology (Brown and Kotler 2004).

Multi-attribute decision making strategies can be broadly classified as either compensatory or non-compensatory (Pitz and Sachs 1984). In non-compensatory strategies, a high value in one attribute overrides all other relevant attributes. For example, a forager might always avoid patches containing predator cues, no matter how rich the patch. In contrast, compensatory strategies involve trade-offs such that a high enough value in a non-preferred attribute can sometimes trump a lower value on a second, preferred attribute. Foraging *Lasius pallitarsis* ants, for example, will chose the patch of highest value, even if it contains a predator, over predator-free alternatives (Nonacs and Dill 1990).

The majority of research on animal foraging preferences has focused on binary decisions, presumably because these are easier to study and model (Schuck-Paim and Kacelnik 2007). However, a binary decision framework is mostly unrealistic in nature, as foragers must often decide between more than two options. This point is trivial if we assume that the choice processes at work are the same irrespective of the number of options. However, work on both humans and animals shows that the size of the choice set indeed matters (Tversky and Simonson 1993; Hurly and Oseen 1999; Bateson et al. 2002; Shafir et al. 2002; Latty and Beekman 2011). Surprisingly, increasing the choice set by adding a new item, even one that is clearly inferior to the two original options, can change the decision-maker's preference between the original alternatives. This peculiar phenomenon is known as a 'context effect' (Tversky and Simonson 1993).

Context effects violate those models of animal and human decision making that assume that decision makers use 'absolute valuation' strategies. Organisms using absolute valuation assign a value to each attribute of interest, sum them, and then choose the option that yields the highest total value (Rapoport 1989). 'Value' is intrinsic to the item, and does not change if other options are included in the choice set. In contrast, context effects are mainly a consequence of comparative valuation strategies, where decision makers rank items based on their value relative to others in the choice set (Tversky 1969a; b; Shafir 1994; Shafir et al. 2002; but see Bateson and Healy 2005 for an alternative view). Context effects have been demonstrated in a wide variety of organisms including humans (Tversky and Simonson 1993), Western honey bees (Shafir et al. 2002), starlings (Bateson 2002), hummingbirds (Hurly and Oseen 1999) and even brainless slime moulds (Latty and Beekman 2011), suggesting that comparative valuation strategies are taxonomically widespread.

The goal of the present study was to examine multi-attribute foraging strategies in the honey bee, *Apis cerana*. Foraging honey bees are excellent models for exploring multi-attribute decision making. Floral resources are characterised by a range of potentially important attributes that may conflict with one another. For example, foragers assess and make trade-offs between the caloric value of the sucrose reward provided by a flower and (1) the effort required to extract that reward (Waddington and Gottlieb 1990; Shafir et al. 2002; Cakmak et al. 2009); (2) the presence of danger at the foraging site (Dukas 2001; Abbott and Dukas 2009); and (3) the presence of toxic chemicals in the nectar (Liu et al. 2006; Tan et al. 2007; Köhler et al. 2012; Tan et al. 2012a).

A hitherto unexplored attribute of honey bee floral choice is nectar temperature. Flowers can increase the temperature of their nectar either through passive heating (Kevan 1975) or the metabolic generation of heat (thermogenesis) (Seymour and Schultze-Motel 1997; Seymour 2001). Although we are unaware of any study showing that honey bee foragers have

preferences for nectar temperatures, other bee species are known to prefer warm nectar over cold nectar (Dyer et al. 2006; Whitney et al. 2008). Indeed, small solitary bees prefer warmer flowers with a low nectar reward over flowers offering a nectar reward at lower temperature (Wilmer 1983).

In this study we explored multi-attribute foraging strategies in *A. cerana*, by examining their relative preferences for sucrose concentration and temperature. Secondly, we determine whether or not honey bee foragers are sensitive to context effects.

Methods

Training: experiments 1–3

The experiments were performed using *A. cerana* colonies in an apiary at the campus of Yunnan Agricultural University, Kunming (102°10′–103°40′ longitude, 24°23′–26°22′ latitude; 1,890 m elevation), China. All colonies were housed in standard Langstroth hives and we equalized the colonies so that each contained two frames of brood and two frames of honey and pollen. The experiments were conducted throughout 2012, from 11:00 to 14:00 on days when the ambient temperature was 15–25 °C, which lies in the range of temperatures at which *A. cerana* colonies actively forage provided the weather is fine (Tan et al. 2012b).

For each of our first three experiments, we studied five colonies on one of 5 consecutive days. For each colony we first trained workers to forage at an artificial feeder resting on a coloured card comprising an inverted 70-ml vial with eighteen 3-mm holes around the lid and containing 30 % w/w sucrose solution situated about 10 m from the colony to be tested. We refilled the feeder as needed to ensure a continuous supply of sucrose solution. We caught departing foragers at the hive entrance and released them slowly at the feeder. Having consumed sufficient sucrose solution, these bees returned to their hive and about 15 min later, newly recruited foragers arrived at the feeder. After 30 foragers were consistently foraging at the training feeder we then replaced the training feeder with two similar feeders 50 cm apart, each resting on a card of the same colour as during the training phase, with various combinations of temperature (10 °C, 15 °C or 30 °C) and sucrose solution concentration (15 % w/w or 30 % w/w). We maintained the experimental temperature of the feeders with identical temperature blocks (OSE-100C, Tiangen, Beijing, China) that accurately maintain temperature in the range 0–100 °C. We monitored the temperature of sugar solution in the feeders using digital thermometer (BAT-12, Sensortek, Moorpark, CA, USA) with a resolution of ±0.1 °C) to ensure that the food temperature did not vary more than 0.5 °C from the desired temperature. We also recorded ambient temperature during each experiment using

a digital thermometer (Sensortek, BAT-12, with a resolution of ±0.1 °C).

Choice tests: experiments 1–3

We observed the feeders for six 3-min periods. During each observation period we counted the number of foragers that landed on each feeder, and the mean length of time for which 9–10 random foragers remained at the feeder for each 3-min observation period. The position of the two feeders was varied in a pseudo-random fashion (avoiding three consecutive tests in the same position) between each observation period to control for potential side preferences. Observation periods were separated by a 5-min break. Prior to and between each observation period, the feeders and the arena were cleaned with distilled water to remove any olfactory cues.

Experiment 1: do foragers consistently prefer higher concentration sucrose solution?

A feeder with 30 % w/w sucrose solution was paired with a feeder containing 15 % sucrose solution, with both feeders held at 10 °C. A second trial was then conducted where the feeders were held at 30 °C. Trials were conducted in September 2012. Ambient temperature ranged between 21 °C and 25 °C.

Experiment 2: do foragers consistently prefer warmer sucrose solution?

We paired two feeders containing a 15 % sucrose solution one held at 10 °C, the other at 30 °C, and recorded bee arrivals as described above. We then repeated the trial, this time with the two feeders containing 30 % sucrose solution. We conducted trials in October and ambient temperature ranged between 20 °C and 23 °C.

Experiment 3: how do foragers trade-off the relative merits of sucrose concentration and food temperature?

We offered the preferred sucrose concentration (30 % w/w) at the less-preferred temperature (10 °C), and the less-preferred sucrose concentration (15 % w/w) with the preferred temperature (30 °C). The aim here was to see how the foragers traded off the relative attractiveness of high sucrose reward and high temperature. We conducted in November; ambient temperatures ranged between 18 °C and 21 °C.

Experiment 4: are the choices made by *A. cerana* foragers context dependent?

To test for context effects, individuals are offered a binary choice consisting of two options that are equally preferred (the 'target' and the 'competitor') or a trinary choice set which contains the target, the competitor and a decoy. The decoy is an item that is inferior (less preferred) than either the competitor or the target. In our experiment, the target feeder contained 30 % w/w sucrose at 15 °C, the competitor contained 15 % w/w sucrose at 30 °C, and the decoy contained 30 % w/w sucrose at 10 °C. Based on pilot experiments, we predicted that preference for the target and competitor would be approximately equal, and that the decoy would be less preferred than either the target or the competitor.

Four individually marked bees from each of five colonies (a total of 20 bees) were trained to forage in a choice arena (70×60×60 cm) located 5 m from the hive. We used the same feeder design as in experiments 1–3, but each feeder type was permanently associated with a different coloured card so that the bees learned to associate a colour with a feeder type. Our experiment was divided into two phases: a training phase, where bees learned to associate colours with a particular combination of heat and sucrose concentration, and a choice phase, where bees were given binary and trinary choice sets. We began the training phase of the experiment once a test bee was reliably entering the arena and feeding. The individual bee was presented with one of our three test feeders: 30 % w/w sucrose at 15 °C (target), a 15 % w/w sucrose at 30 °C (competitor) or a 30 % w/w sucrose at 10 °C (decoy) on each trip. The feeder types were presented in random order. Each bee visited each feeder type ten times making a total of 30 training trips. By the end of this training, we assumed that the bee had learned to associate each feeder type to the appropriate colour. We test this assumption in experiment 5. The training process typically lasted 2 days.

During the choice phase, we presented individual foragers with either a trinary (target, competitor, decoy) or a binary (target and competitor) choice set haphazardly. Since the presence of conspecifics might affect choice behaviour, we only allowed one bee into the arena at a time. Each bee made ten visits to the choice arena. Experiments were conducted in December; ambient temperature was between 15 °C and 18 °C.

Experiment 5: can honey bees learn to associate a temperature/sucrose concentration with a colour?

A central assumption of our context dependency study (experiment 4) is that a foraging bee can learn to associate a specific combination of sucrose and temperature with a colour. To test this assumption we trained individually marked bees to enter an arena as described above. After a bee was regularly entering the arena we offered a feeder containing either 30 °C, 15 % ww sucrose resting on a red card or 15 °C, 30 % sucrose resting on a blue card. We randomly offered the two kinds of feeders for ten trips so that the bee visited each type of feeder five times. Following training, and on the bee's

11th trip, we offered a feeder containing 20 % ww sucrose at 20 °C at two feeders, one resting on a red card and one resting on a blue card. If the bees had learned to associate their preferred temperature–concentration combination with a colour, they should preferentially land on the colour of their preference that they had learned during training. The training and test was repeated for each of ten bees.

To exclude the possibility that the bees had a colour preference, we repeated this experiment with the opposite training colours. That is, during training the 30 °C, 15 % feeder rested on a blue card, and the 15 °C, 30 % sucrose feeder rested on a red card.

Statistics

For experiments 1–3, we analysed the number of visits per 3-min period and the mean duration of imbibing of ten random bees, as separate two-way repeated-measures analyses of variance (ANOVAs). Each 3-min period was regarded as a repeated measure, and colonies were replicates. Data were tested for equality of variances across feeders using Levene's tests, but no significant violations were detected.

In experiment 4, we were interested in determining if foragers were susceptible to context effects. Context effects violate one of the key principles of economic rationality: independence of irrelevant alternatives (IIA) (Luce 1959). One version of IIA, known as regularity, holds that the absolute preferences of a forager will not increase with the addition of a decoy. Here, regularity would be violated if the absolute proportion of honey bees choosing the target increased in the trinary trials.

The second version of IIA, the constant ratio rule, states that the relative proportion of choices made between two options will not change when a decoy item is added to the choice set (Luce 1959). This can occur if, for example, the decoy competes more with the competitor, resulting in the competitor losing greater market share when the decoy is introduced to the choice set. Following Bateson et al. (2002), we calculated relative preference for the target as:

$$\frac{\text{Proportion visits to Target} - \text{Proportion visits to Competitor}}{\text{Proportion visits to Target} + \text{Proportion visits to Competitor}}$$

The resulting preference value ranges from −1 to +1. A value of −1 indicates 0 choices in favor of the target, while a score of +1 indicates that the target was selected 100 % of the time. A value of 0 indicates that choices were divided equally between the target and the competitor. Relative preference has the benefit of being more sensitive to changes in preference in situations where the decoy option is occasionally selected (Bateson et al. 2002).

We tested the hypothesis that adding a decoy to the choice set changed the bees' absolute and relative preference for the target (regularity and the constant ratio rule, respectively) by measuring the proportion of visits individual bees made to the target feeder over their ten flights. Each bee therefore contributed a single data point. We tested for violations of regularity and the constant ratio rule using repeated-measures ANOVAs, with either the absolute or relative proportion of visits to the target as our dependent variables.

We were also interested in detecting context effects at the individual level. We tested for preference reversals (switching from a preference for the target in the binary trials, to a preference for B in the trinary trials) using binomial tests (expected probability=0.5 in the binary trials, and 0.33 in the trinary trials). Preference reversals violate both regularity and the constant ratio rule and are strong evidence of context effects.

In experiment 5, we tested the null hypothesis that each trained bee would land on the feeder resting on the blue or red card with equal frequency using a binomial test.

Data are presented as treatment means and standard error of the means.

Results

Experiment 1: do foragers consistently prefer higher concentration sucrose?

Averaged over replicate trials and colonies, foragers preferred more concentrated sucrose syrup at both 10 °C and 30 °C as measured by the number of bee visits per 3 min and the length of time a bee spent imbibing syrup (Figs. 1 and 2). There were significantly fewer visits at 15 °C than at 30 °C ($F_{1,16}$=23.88, $P<0.001$), and a significant interaction between temperature and concentration ($F_{1,16}$=5.85, $P=0.028$) caused by the smaller number of visits to 30 % syrup at 30 °C than at 15 °C. There was no significant difference in imbibing time across concentrations ($F_{1,16}$=1.92, $P=0.18$), nor was there a significant interaction between temperature and concentration ($F_{1,16}$=0.07, $P=0.79$). Replicate trials were not a significant factor for the number of visits ($F_{5,80}$=0.14, $P=0.98$) or the imbibing time ($F_{5,80}$ 1.61, $P=0.17$).

Experiment 2: do foragers consistently prefer warmer food?

Averaged over replicate trials, foragers preferred warmer sucrose solution both when the solution was dilute (15 %) and concentrated (30 %) as measured by the number of bee visits per 3 min and the length of time a bee spent imbibing syrup (Figs. 1 and 2). There were significantly fewer visits when the syrup offered contained 15 % sucrose ($F_{1,16}$=20.65, $P<0.001$), but no significant interaction between temperature and concentration ($F_{1,16}$=0.24, $P=0.63$). The imbibing time was significantly longer at 30 °C than at 10 °C ($F_{1,16}$=275.38, $P<0.001$), and there was a marginally significant interaction between

Fig. 1 Number of bee visits per 3 min at feeders containing sucrose solution at two temperature and concentration combinations. Means and standard errors are derived from a repeated-measures ANOVA of six observation periods across five replicate colonies. ***The two means are significantly different at $P<0.001$. **The two means are significantly different at $P<0.01$. Error bars represent standard errors
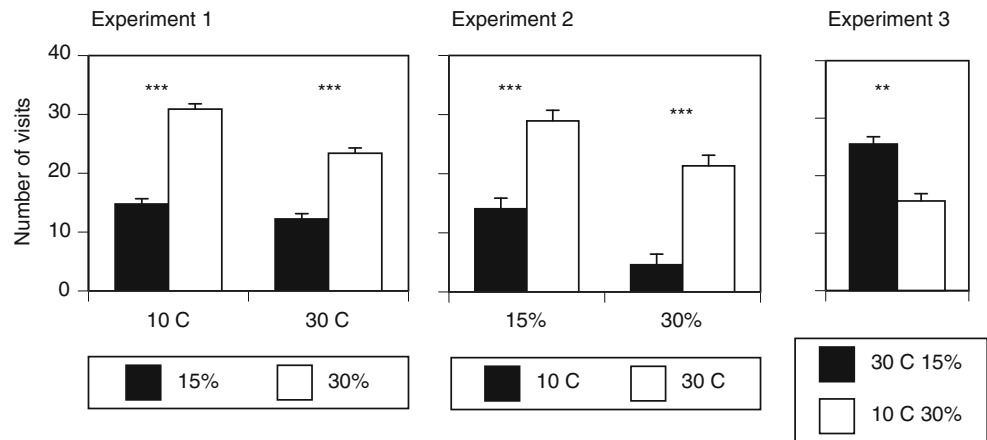
concentration and temperature ($F_{1,16}=4.55$, $P=0.05$). Replicate trials were not a significant factor for imbibing time ($F_{5,80}=0.84$, $P=0.52$), though they were for number of visits ($F_{5,80}=3.0$, $P=0.016$).

Experiment 3: what is the relative value of warmth and sucrose concentration?

When offered the choice of cold concentrated sucrose solution and warm dilute solution, foragers favored warmth over sucrose concentration (Figs. 1 and 2). There was no significant effect of replicate trial on imbibing time ($F_{5,40}=0.62$, $P=0.69$) or the number of visits ($F_{5,40}=0.60$, $P=0.70$).

Experiment 4: are the choices made by foragers context dependent?

Bees selected the target (30 % w/w sucrose at 15 °C) more often than the competitor (15 % w/w sucrose at 30 °C) in both the binary and the trinary trials (Fig. 3; Binary trials: Welch's test: $F_{1,19}=245.41$, $P<0.001$; trinary trials: $F_{1,19}=265.75$, $P<0.001$). Adding a decoy (30 % w/w sucrose at 10 °C) had no effect on the bees' absolute preference for the target ($F_{1,19}=2.1$, $P=0.153$). However, the presence of the decoy resulted in

a significant decrease in absolute preference for the competitor, which fell from being selected a mean 0.25 ± 0.02 in the binary trials to 0.07 ± 0.01 in the trinary trials ($F_{1,19}=30.71$, $P<0.001$). Similarly, the relative preference for the target over the competitor increased significantly when the decoy was added to the choice set (Fig. 4; $F_{1,19}=23.14$, $P<0.001$).

In the binary trials, 16 of the 20 bees had a significant preference for the target ($P<0.05$, binary test, expected probability 0.5), three bees had non-significant preferences for the target, and one bee chose the target 50 % of the time. In the trinary trials, 16 bees had a significant preference ($P<0.05$) for the target, two had a non-significant preference for the target, and two had a non-significant preference for the decoy. We found no evidence of preference reversals, as no bees preferred the competitor in the trinary trial.

Experiment 5: can bees associate a temperature/sucrose concentration with a colour?

In this experiment foragers showed a preference for 30 % sucrose at 15 °C over 15 % sucrose at 30 °C. In the 11th visit, bees preferred the colour that they had learned to associate with the 30 % at 15 °C combination. When the preferred combination was associated with the blue card during training,

Fig. 2 Experiment 2. Imbibing time of ten random bees at feeders containing sucrose solution at two temperature and concentration combinations. Means and standard errors are derived from a repeated-measures ANOVA of six observation periods across five replicate colonies. ***The two means are significantly different at $P<0.001$. **The two means are significantly different at $P<0.01$. Error bars represent standard errors
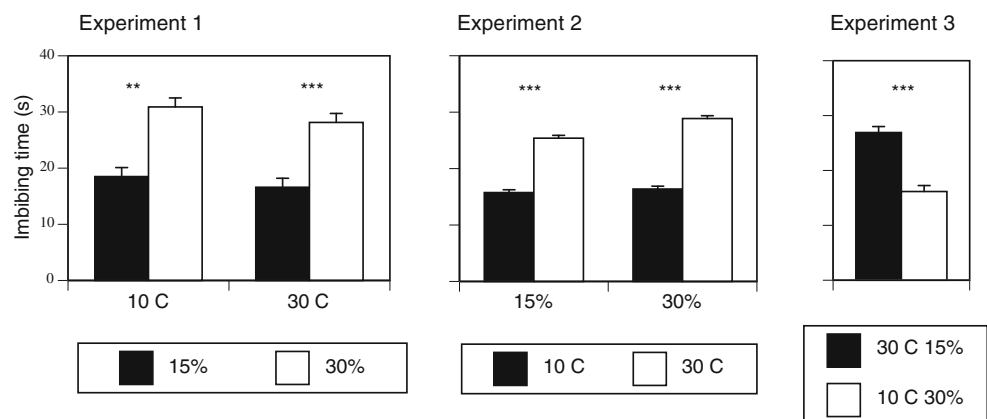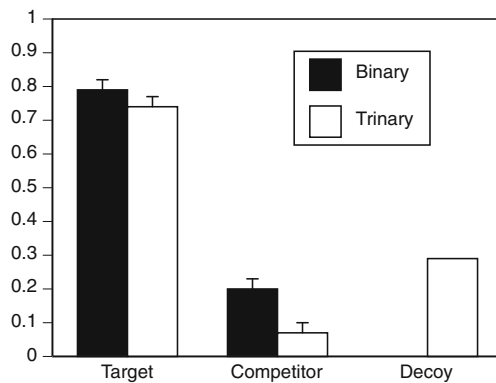
Fig. 3 The effect of a decoy feeder (30 % sucrose, 10 °C) on the proportion of bee visits to the Target feeder (30 % sucrose, 15 °C) and the Competitor feeder (15 % sucrose at 30 °C). *Black bars* indicate the mean preference of bees in binary trials; *grey bars* indicate mean bee preferences during trinary trials. Ten bees were used in the trials. Error bars represent standard errors

ten out of ten bees ($P<0.00001$) chose the blue card on the 11th trip. When the preferred combination was associated with red cards, eight out of ten bees opted for red cards ($P=0.04$) on the 11th trip. The result is statistically similar, regardless of which training colour was associated with the preferred reward (χ_1^2 test of heterogeneity$=0.80$, $P=0.37$).

Discussion

In binary choice trials, groups of 30 foragers consistently preferred warm solution over cool solution (when both solutions had the same concentration) and concentrated solution over dilute solution (when both solutions were held at the same temperature). If bees were using a non-compensatory strategy, we would expect them to consistently prioritise one attribute over the other. For example, bees might always choose the feeder with the highest sucrose concentration, irrespective of its temperature. However, data from experiments 3 and 4 suggest that honey bees use a compensatory
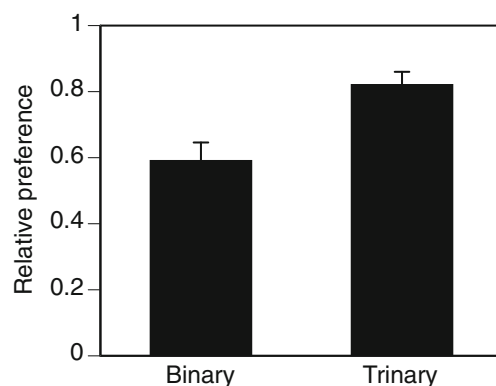

Fig. 4 Change in mean relative preference for the target. Bars are standard errors

strategy by making trade-offs between temperature and sucrose concentration. In experiment three, bees preferred the warmer, dilute feeder (15 % w/w at 30C) over the more concentrated, but cooler feeder (30 % w/w at 10 °C). However, in experiment 4, individual bees preferred the more concentrated, cool feeder (30 % w/w at 15 °C) feeder over a warmer, more dilute feeder (15 % w/w at 30 °C). Our results suggest that if sucrose concentration is sufficiently high, and the difference between temperatures is relatively small, bees will select the higher concentration feeder even if it contains cooler syrup. In addition, our trinary trials show that honey bee preferences can be influenced by context effects, as the relative preference for the competitor feeder decreased when a decoy was added to the choice set, thus violating the constant ratio rule. In essence, the addition of the decoy feeder increased relative preference for the target by stealing a disproportionate amount of 'market share' from the competitor.

The widespread occurrence of context effects (including in a closely related bee species, the western honey bee; Shafir et al. 2002) suggests that many organisms use comparative valuation strategies. This raises the question: why are comparative valuation strategies so common in nature? Researchers seeking to answer this question typically fall into two groups: those that suggest that context effects occur due to constraints on the way biological systems process information, and those that suggest that the comparative valuation strategies underlying context effects have some adaptive value. Using mathematical models of decision making, Nicolis et al. (2011) suggested that context effects will always arise when a decision-making system is based on positive feedback. Positive feedback occurs when a change in a system is self-reinforcing (Camazine et al. 2001), and is implicated as the mechanism behind decision making processes in brains (Deco et al. 2009), colonies of social insects (Beckers et al. 1990; Nicolis and Deneubourg 1999; Sumpter and Pratt 2003; Sumpter 2006), and foraging slime moulds (Tero et al. 2010; Latty and Beekman 2011). Alternatively, comparative valuation strategies may be favored by natural selection because they produce similar outcomes to absolute valuation, but with less computational effort (Gigerenzer 1997). Indeed, a recent modelling study found that comparative valuation strategies can outperform strategies based on absolute valuation under a number of environmental assumptions (Waksberg et al. 2009).

In our binary trials, *A. cerana* workers selected warmer nectar over cooler nectar. The nectar preferences of foraging bees are influenced by the interaction between nectar temperature, metabolic requirements and environmental temperature. For example, the stingless bee, *Tetragonula carbonaria*, modulates its nectar temperature preferences according to the ambient temperature in its environment (Norgate et al. 2010). Our experiments were conducted under field conditions, and it is possible that the observed trade-off between warmth and sucrose concentration was driven by differences

in ambient air temperature. However, experiment 4, where bees prioritised sucrose concentration over warmth, was conducted during cooler weather (15–18 °C) then experiment 3, where bees prioritized warmth (18–21 °C). If ambient air temperature was a driving factor, than we would have expected the opposite pattern: bees should prioritise warmth when ambient air temperature is cooler. We therefore conclude that ambient temperatures alone do not explain the bees switch from prioritizing warmth to preferring sucrose concentration.

Relative to other bees, *A. cerana* has a low thoracic temperature during foraging (Tan et al. 2012b), and imbibing cool nectar may push foragers into a zone of hypothermia that prevents them from returning to the colony. Even endotherms like hummingbirds pay a significant metabolic cost when they imbibe cold nectar (Lotz et al. 2003). Thus, *A. cerana* foragers may increase their metabolic efficiency (and lower their risk of hypothermia) by prioritizing nectar temperature over sucrose concentration unless sucrose concentration is high and the difference in temperatures is relatively small. Indeed, in our experiment foragers always imbibed cooler syrup for shorter periods than they did warmer syrup (Figs. 1 and 2).

A. cerana's general preference for warm nectar (given similar sucrose concentration) could have mechanistic explanations beyond the management of thermal efficiency. Warm flowers produce more nectar with a higher sugar concentration than cooler flowers (Corbet 1978), so warm temperatures may serve as a cue indicating high quality food resources. Bumble bees can be trained to associate temperature with nectar quality (Whitney et al. 2008), reinforcing the idea that temperature can be used by foragers as a cue of quality. Temperature can influence the viscosity of nectar such that warmer nectars are less viscous and easier to imbibe (Roubik and Buckman 1984). Temperature might also affect the way in which sucrose concentration is perceived. In humans, for example, sucrose receptors in the tongue are influenced by temperature. As a result, heat makes sweet food taste sweeter (Bartoshuk et al. 1982). If the sucrose receptors of bees are similarly unbuffered, modelling suggests that plants could 'cheat' pollinators by using heat to increase the perceived quality of their nectar rewards (Whitney et al. 2008). Understanding the specific trade-offs individual bees make between sucrose and temperature can therefore impact our understanding of the co-evolution of plants and pollinators.

Honey bees can readily learn to associate warmth (Hammer et al. 2009), colour (Frisch 1967), shapes (Frisch 1967) and even abstract concepts (Avarguès-Weber et al. 2012) with a food reward, so we were confident that the trained bees could associate the training colour with the correct temperature/concentration combination in experiment 4. Data from experiment 5 supports this expectation. Thus, the critical assumption of experiment 4 (that the bees knew which syrup was in which feeder based on the colour of the card it rested on) is supported. This ability also adds to the growing list of examples showing that honey bees can learn tasks that involve integrating more than one variable (e.g., Srinivasan et al. 1998; Giurfa et al. 2001; Chen et al. 2003; Zhang et al. 2004; Reinhard et al. 2006).

Experiments 1–3 were conducted with groups of 30 workers. It is possible that the behaviour of individual workers was influenced by the presence of other bees at the feeders. Nonetheless we find a strong effect of both temperature and sucrose concentration on the number of bee visits to each feeder, and the length of time spent at feeders. These group results are exactly mirrored by the behaviour of individual bees in experiment 4.

Decision making while foraging is computationally difficult, but can be facilitated by absolute rules that prioritize the attributes (e.g., quality, ease of harvest, presence of danger and temperature) of a food source. However, where the decision making process is based on comparative valuation, the outcome of the decision making process is complicated by the presence of alternatives in the choice set, resulting in inconsistent preferences between binary and trinary trials. Thus the size and composition of the specific choice set may be a key variable to consider when assessing honey bee flower preferences. While we have demonstrated that bees use a compensatory strategy when faced with feeders that differ in sucrose concentration and warmth, honey bees could use noncompensatory strategies when assessing other attributes such as the risk of predation (Dukas 2001; Abbott and Dukas 2009). We predict that in this case, foragers would not be influenced by decoy choices, and would invariably avoid predators, whatever other choices are available to them. This hypothesis remains to be tested.

References

Abbott KR, Dukas R (2009) Honeybees consider flower danger in their waggle dance. Anim Behav 78:633–635

Avarguès-Weber A, Dyer AG, Combe M, Giurfa M (2012) Simultaneous mastering of two abstract concepts by the minature brain of bees. Proc Natl Acad Sci U S A 109:7481–7486

Bartoshuk LM, Rennert K, Rodin J, Stevans JC (1982) Effects of temperature on the perceived sweetness of sucrose. Physiol Behav 28:905–910

Bateson M (2002) Context-dependent foraging choices in risk-sensitive starlings. Anim Behav 64:251–260

Bateson M, Healy SD (2005) Comparative evaluation and its implications for mate choice. Trends Ecol Evol 20:659–664

Bateson M, Healy SD, Hurly TA (2002) Irrational choices in hummingbird foraging behaviour. Anim Behav 63:587–596

Beckers R, Deneubourg JL, Goss S, Pasteels JM (1990) Collective decision making through food recruitment. Ins Soc 37:258–267

Brown JS, Kotler BP (2004) Hazardous duty pay and the foraging cost of predation. Ecol Let 7:999–1014

Cakmak I, Sanderson C, Blocker TD, Pham LL, Checotah S, Norman AA, Harader-Pate BK, Reidenbaugh RT, Nenchev P, Barthell JF, Wells H (2009) Different solutions by bees to a foraging problem. Anim Behav 77:1273–1280

Camazine S, Deneuborg JL, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton, NJ

Chen L, Zhang SW, Srinivasan MV (2003) Global perception in small brains: topological pattern recognition in honey bees. Proc Natl Acad Sci U S A 100:6884–6889

Corbet SA (1978) Bee visits and the nectar of Echium vulgare L. and Sinapis alba L. Ecol Entomol 3:25–37

Deco G, Rolls ET, Romo R (2009) Stochastic dynamics as a principle of brain function. Prog Neurobiol 88:1–16

Dukas R (2001) Effects of perceived danger on flower choice by bees. Ecol Let 4:327–333

Dyer AG, Whitney HM, Arnold SEJ, Glover BJ, Chittka L (2006) Bees associate warmth with floral colour. Nature 442:525

Kv F (1967) The dance language and orientation of bees. Harvard University Press, Cambridge

Gigerenzer G (1997) Rounded rationality: Models of fast and frugal inference. Swiss J Econ Stat 133:201–218

Giurfa M, Zhang SW, Jenett A, Menzel R, Srinivasan MV (2001) The concepts of 'sameness' and 'difference' in an insect. Nature 410:930–933

Hammer TJ, Hata C, Nieh JC (2009) Thermal learning in the honeybee, Apis mellifera. J Exp Biol 212:3928–3934

Hurly TA, Oseen MD (1999) Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. Anim Behav 58:59–66

Kevan PG (1975) Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. Science 189:723–726

Köhler A, Pirk CWW, Nicolson SW (2012) Honeybees and nectar nicotine: deterrence and reduced survival versus potential health benefits. J Ins Physiol 58:286–292

Latty T, Beekman M (2010) Food quality and the risk of light exposure affect patch-choice decisions in the slime mould Physarum polycephalum. Ecology 91:22–27

Latty T, Beekman M (2011) Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. Proc Roy Soc B 278:307–312

Liu F, Chen J, Chai J, Zhang X, Bai X, He D, Roubik DW (2006) Adaptive functions of defensive plant phenolics and a non-linear bee response to nectar components. Func Ecol 21:96–100

Lotz CN, del Rio CM, Nicolson SW (2003) Hummingbirds pay a high cost for a warm drink. J Comp Physiol B 173:455–462

Luce RD (1959) Individual choice behavior: a theoretical analysis. Wiley, New York

McArthur C, Orlando P, Banks PB, Brown JS (2012) The foraging tightrope between predation risk and plant toxins: a matter of concentration. Func Ecol 26:74–83

Nicolis SC, Deneubourg JL (1999) Emerging patterns and food recruitment in ants: an analytical study. J Theor Biol 198:575–592

Nicolis SC, Zabzina N, Latty T, Sumpter DJT (2011) Collective irrationality and positive feedback. PLoS One 6:e18901. doi:10.1371/journal.pone.0018901

Nonacs P, Dill LM (1990) Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. Ecology 71:1886–1892

Norgate M, Boyd-Gerny S, Simonov V, Rosa MGP, Heard TA, Dyer AG (2010) Ambient temperature influences Australian native stingless bee (Trigona carbonaria) preference for warm nectar. PLoS ONE 5(8):doi:10.1371/journal.pone.0012000

Pitz GF, Sachs NJ (1984) Judgement and decision: theory and application. Annu Rev Psychol 35:139–164

Rapoport A (1989) Decision theory and decision behaviour. Kluwer Academic Publishers, London

Reinhard J, Srinivasan MV, Zhang SW (2006) Complex memories in honeybees: can there be more than two? J Comp Physiol A 192:409–416

Roubik DW, Buckman SL (1984) Nectar selection by Melipona and Apis mellifera (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. Oecologia 61:1–10

Schuck-Paim C, Kacelnik A (2007) Choice processes in multialternative decision making. Behav Ecol 18:541–550

Seymour RS (2001) Biophysics and physiology of temperature regulation on thermogenic flowers. Bioscience Reports 21:223–236

Seymour RS, Schultze-Motel P (1997) Heat-producing flowers. Endeavour 21:125–129

Shafir S (1994) Intrasitivity of preferences in honey bees: support for 'comparative' evaluation of foraging options. Anim Behav 48:55–67

Shafir S, Waite TA, Smith BH (2002) Context-dependent violations of rational choice in honeybees (Apis mellifera) and gray jays (Perisoreus canafensis). Behav Ecol Sociobiol 51:180–187

Simpson SJ, Sibly RM, Lee KP, Behmer ST, Raubenheimer D (2004) Optimal foraging when regulating uptake of multiple nutrients. Anim Behav 68:1299–1311

Srinivasan MV, Zhang SW, Zhu H (1998) Honeybees link sights to smells. Nature 396:637–638

Sumpter DJT (2006) The principles of collective animal behaviour. Phil Trans Biol Sci 361:5–22

Sumpter DJT, Pratt SC (2003) A modelling framework for understanding social insect foraging. Behav Ecol Sociobiol 53:131–144

Tan K, Guo YH, Nicolson SW, Radloff SE, Song QS, Hepburn HR (2007) Honeybee (Apis cerana) foraging responses to the toxic honey of Tripterygium hypoglaucum (Celastraceae): changing threshold of nectar acceptability. J Chem Ecol 33:2209–2217

Tan K, Wang Z, Yang M, Fuchs S, Luo L, Zhang Z, Li H, Zhuang D, Yang S, Tautz J, Beekman M, Oldroyd BP (2012a) Asian hive bees, Apis cerana, modulate dance communication in response to nectar toxicity and demand. Anim Behav 84:1589–1594

Tan K, Yang S, Wang Z-W, Radloff SE, Oldroyd BP (2012b) Differences in foraging and broodnest temperature in the honey bees Apis cerana and A. mellifera. Apidologie 43:618–623

Tero A, Takagi S, Saigusa T, Ito K, Bebber DP, Fricker MD, Yumiki K, Kobayashi R, Nakagaki T (2010) Rules for biologically inspired adaptive networks. Science 327:439–442

Tversky A (1969a) Intrasitivity of preferences. Psych Rev 76:31–48

Tversky A (1969b) Substitutibility and similarity in binary choices. J Math Psychol 6:1–12

Tversky A, Simonson I (1993) Context-dependent preferences. Manag Sci 39:1179–1189

Waddington KD, Gottlieb N (1990) Actual vs. perceived profitability: a study of floral choice by honey bees. J Insect Behav 3:429–441

Waksberg AJ, Smith AB, Burd M (2009) Can irrational behaviour maximise fitness? Behav Ecol Sociobiol 63:461–471

Webster SJ, Dill LM (2006) The energetic equivalence of changing salinity and temperature to juvenile salmon. Func Ecol 20:621–629

Whitney HM, Dyer AG, Chittka L, Rands SA, Glover BJ (2008) The interaction of temperature and sucrose concentration preferences in bumblebees. Naturwissenschaften 95:845–850

Wilmer PG (1983) Thermal constraints on activity patterns in nectar-feeding insects. Ecol Entomol 8:455–469

Zhang SW, Srinivasan MV, Zhu H, Wong J (2004) Grouping of visual objects by honeybees. J Exp Biol 207:3289–3298