

Phantom alternatives influence food preferences in the eastern honeybee *Apis cerana*

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Summary

1. Most models of animal choice behaviour assume that desirable but unavailable options, such as a high quality, but inhabited nest sites, do not influence an individual's preferences for the remaining options. However, experiments suggest that in mammals, the mere presence of such 'phantom' alternatives can alter, and even reverse, an individual's preferences for other items in a choice set.

2. Phantom alternatives may be widespread in nature, as they occur whenever a resource is visible, but unavailable at the time of choice. They are particularly relevant for nectar-foraging animals, where previously rewarding flowers may sometimes be empty. Here, we investigate the effect of phantom alternatives on feeder preferences in the eastern honeybee, *Apis cerana*.

3. First, we tested the effects of unattractive and attractive phantom alternatives by presenting individual bees with either a binary choice set containing two feeders that differed strongly in two qualities, but were equally preferred overall ('option 1' and 'option 2'), or a ternary choice set containing option 1, option 2 and one of two phantom types (unattractive and attractive). Secondly, we determined whether phantoms increase (similarity effect) or decrease (dissimilarity effect) preference for phantom-similar choices.

4. In binary trials, bees had no significant preference for option 1 or option 2. However, after encountering an attractive phantom alternative, individual bees preferred option 2. The unattractive phantom did not influence bee preferences. Phantoms consistently changed individual bee preferences in favour of the phantom-similar choice. This means that the presence of an attractive food source, even if it is unavailable, can influence preference relationships between remaining items in the choice set.

5. Our findings highlight the importance of considering the potential for phantom effects when studying the foraging behaviour of animals. Our results are particularly relevant for nectarivores, where empty but previously rewarding flowers are a common occurrence. Since an increase in pollinator visits can result in higher seed set, our results open up the possibility that by shifting pollinator preferences, empty flowers could have otherwise-unpredicted influences on community composition, plant–pollinator interactions and pollinator behaviour.

Key-words: choice, cognition, decision-making, foraging preferences, honeybee, indifference to irrelevant alternatives, phantom alternatives

Introduction

Animals living in complex environments are constantly faced with decisions such as what to eat, what partner to

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mate with and where to live. Decisions can be complicated by the fact that options can vary in a number of important features, some or all of which might be important to the animal. Foragers, for example, may simultaneously consider caloric value, macronutrient content (Simpson & Raubenheimer 1995), predation risk (Dukas & Morse 2003, Brown & Kotler 2004; While & McArthur 2005) and ease of handling (Shafir 1994) when deciding among food items. In some cases, attributes might conflict, for example, when the best quality food patch also has the highest predation risk. Individual preferences for food and habitat directly affect the distribution of individuals, and in doing so, mediate interindividual interactions such as competition, herbivory and predation. Understanding how animals make multi-attribute decisions is therefore central to the discipline of foraging ecology (Brown & Kotler 2004).

Most models of animal and human multi-attribute choice make the implicit assumption that an individual's preference for a particular item does not change when irrelevant items are added to the choice set (Luce 1959; Rapoport 1989). In humans, this axiom is often violated by a peculiar phenomenon known as the 'phantom alternative effect' where, for example, the presence of a sold out or otherwise unavailable item changes an individual's preferences for other items in a choice set (Pratkanis & Farquhar 1992; Farquhar & Pratkanis 1993; Doyle *et al.* 1999; Pettibone & Wedell 2000; Ge, Messinger & Li 2009). Phantom alternatives are items that 'appear real, but which are unavailable at the time of choice' (Pratkanis & Farquhar 1992). Familiar human examples abound: attempting to purchase a cheap flight online only to be told that it is 'sold out' after you have selected it, real estate listings that contain properties boldly stamped with a 'sold' sticker and job candidates who withdraw from the selection process. In animal ecology, phantom alternatives occur whenever a resource is visible, but unavailable at the time of choice. Examples might include a pair-bonded mate, a preferred but inhabited nest site, or an already parasitized host. For nectar foragers, phantoms occur when previously rewarding flowers are unexpectedly empty of nectar, or when nectarless flowers mimic rewarding flowers. The experience of a bee that lands on a normally rewarding flower only to find it is empty may be analogous to the situation of a human consumer arriving at a shop intent on purchasing a heavily advertised desirable product only to find that the product has been sold out.

Research on human consumers indicates that phantoms generally (but not always) function by increasing preference for items similar to the phantom (Ge, Messinger & Li 2009). This has been termed the 'similarity effect'. The most intuitively appealing explanation for the similarity effect suggests that, when faced with a sold out item, consumers simply 'replace' the sold out product with whichever item of the remaining choices is most similar to the one they originally wanted (Pettibone & Wedell 2000). In

effect, phantoms 'prime' shoppers to prefer particular attributes over others. Similarity effects have also been documented in non-human animals. Scarpi (2011) found that when domestic cats were presented with phantom feeders that had previously contained a particular combination and concentration of meats, the cats preferred alternative feeders that were most similar to the unavailable phantom.

In contrast, dissimilarity effects have occasionally been reported where the presence of a sold out item causes shoppers to avoid items that share similar characteristics to the unavailable product (see examples in Fitzsimons 2000). Dissimilarity effects have not yet been described in animals, but could potentially occur if individuals that encounter an unrewarding item (such as an empty flower) avoid other items with similar characteristics. For example, after encountering an empty red flower, a forager might subsequently avoid all red flowers.

Phantom alternatives may be a frequent phenomenon for nectivorous animals, since they are usually unable to detect the presence of nectar before entering a flower (Thakar *et al.* 2003). Empty flowers can be surprisingly common: one study found that 46% of *Lotus coriculatus* flowers at a site in California were empty in the morning, before being visited by bees (Wetherwax 1986). Further, a field study found that 24 of 28 plant species (85%) contained at least some individuals that did not produce nectar (Thakar *et al.* 2003). Several studies have examined the impact of empty flowers on pollinator behaviour, but these studies have focused on how empty flowers influence a pollinator's likelihood of abandoning an inflorescence (for example, Johnson 2000, Biernaskie, Cartar & Hurlly 2002; Smithson & Gigord 2003; Bailey *et al.* 2007). In contrast, the phantom alternative effect is concerned with how encounters with an empty flower influence preference relationships among other flower species in the community.

Here, we study phantom alternative effects in a nectivorous insect, the eastern honeybee, *Apis cerana*. Two types of phantoms have been reported in the literature: attractive phantoms and unattractive phantoms (Pratkanis & Farquhar 1992). Attractive phantoms are more desirable than all other items in the choice set, while unattractive phantoms are less desirable than all other items in the choice set. Both types of phantom alternative can influence choice in humans (reviewed in Pratkanis & Farquhar 1992; Doyle *et al.* 1999; Ge, Messinger & Li 2009), although attractive phantoms seem to have a stronger influence.

We determined the effects of unattractive and attractive phantoms by presenting individual bees with either a binary choice set containing two feeders that differed strongly in two qualities, but were equally preferred overall ('option 1' and 'option 2'), or ternary choices in which the same, option 1 and option 2 were presented along with a phantom alternative (an empty feeder that had previously contained a reward). All three feeders and their

contents were familiar to the bees. We predicted that bees, like the majority of humans, would show preference changes after experiencing an attractive phantom, but not after encountering an unattractive phantom. We also determined whether phantoms change preferences by increasing preference towards the item that was most similar (similarity effect) or least similar (dissimilarity effect) to the phantom.

Methods

STUDY ORGANISMS

We used *A. cerana* colonies situated at an apiary on the campus of Yunnan Agricultural University, Kunming (102°10'–103°40' longitude, 24°23'–26°22' latitude, 1890 m elevation), China. All colonies were kept in standard Langstroth hives, each containing two frames of brood and two frames of honey/pollen. Experiments 1a and 1b were conducted in March and April 2013, Experiment 2 in August 2013 and Experiment 3 in October and November 2013. All experiments took place from 11:00 to 14:00 on days when the ambient temperature was between 20 and 29 °C, which is within the range of temperatures at which *A. cerana* colonies actively forage (Tan *et al.* 2012).

GENERAL DESIGN

Context effects are usually studied using a design where individuals are presented with either a binary choice set containing two options (option 1 and option 2), or a ternary choice set containing option 1, option 2 and a new decoy item (Tversky & Simonson 1993; Bateson 2002; Bateson, Healy & Hurly 2002; Latty & Beekman 2011). If bees obey the principle of indifference to irrelevant alternatives, then, their preference for option 1 should not change when the decoy is added to the choice set. Context effects are only expected to occur when individuals face multi-attribute choices (but see Morgan *et al.* 2012). In our experiments, we used feeders that differed in two attributes: sucrose concentration and temperature. We chose these two attributes because our earlier studies (Tan *et al.* 2014b) found that they elicit context effects in *A. cerana*.

Bees were presented with aluminium feeders that sat atop a temperature block (OSE-100C; Tiangen, Beijing, China) that accurately maintained temperatures in the range 0–100 °C. There were six small pits in the feeder each capable of holding 1.5 mL of sugar water. We determined that the sucrose solution did not vary more than 0.5 °C from the desired temperature by monitoring the temperature with a digital thermometer (BAT-12; Sensortek, Moorpark, CA, USA) with a resolution of ± 0.1 °C. We also recorded ambient temperature using a digital thermometer. The feeders were located in a choice arena consisting of an open-top cardboard box (70 cm \times 60 cm \times 60 cm) 5 m from the hive.

TRAINING PHASE

In order to determine each bee's feeder preference, we needed to train individual bees to associate each combination of sucrose concentration and temperature with a specific colour. We randomly associated each sucrose concentration/temperature combination with a specific colour by placing the feeder on

top of a coloured card (red, blue, green or yellow). The feeder colour associated with each particular sucrose concentration/temperature combination was changed randomly between individuals. We marked each bee with a numbered bee tag (Opalith-Zeichenplättchen) affixed to the thorax with shellac. We trained bees to forage in the choice arena by catching departing foragers at the hive entrance and gently transporting them to the choice arena where they were slowly released beside one of the three feeder types. This procedure had the additional beneficial effect of preventing non-focal bees from entering the arena, as only trained bees were aware of the feeder's presence. Each time the focal bee entered the arena, it was randomly presented with one of the three feeder types. Training continued until the bee had visited each feeder type 10 times. Our previous studies have shown that this training procedure is highly effective so that bees strongly associate training colour with a particular sucrose concentration/temperature combination after 10 trips (Tan *et al.* 2014b). The training process typically lasted 2 days per bee.

CHOICE TESTS

To test for the phantom alternative effect, we needed to create a situation analogous to the human experience of selecting an item only to find out it is no longer available. We made the phantom 'unavailable' by removing the sucrose solution and ensuring that the heating block was turned off and the feeder platform was at ambient temperature. Otherwise, the phantom feeder was visually identical to the rewarding feeder used during training. Bees were unable to ascertain the unrewarding nature of the phantom until they landed on and antennated the feeder.

Individual foragers that had been trained to associate colour with a particular temperature/sucrose concentration combination were allowed into the choice arena that contained either the binary choice set (option 1 and option 2) or ternary choice set (option 1, option 2 and the phantom). We counted the number of times each bee visited each feeder type over 10 consecutive visits. A 'visit' was defined as a bee alighting on the feeder adjacent to one of the syrup-filled pits and remaining there for more than 15 s. Relative feeder positions were randomized between visits. Different bees were used in each experiment so that bees were never reused.

EXPERIMENT 1. DO PHANTOM ALTERNATIVES CHANGE FORAGER PREFERENCES?

General procedure

We determined whether the presence of attractive or unattractive phantoms influenced forager preference for option 1 or option 2. We used four different feeder types: option 1 (15% w/w sucrose at 30 °C), option 2 (30% sucrose w/w at 10 °C), an unattractive alternative (10% w/w sucrose at 30 °C) and an attractive alternative (30% w/w at 30 °C) (Fig. 1). Based on previous experiments (Tan *et al.* 2014b), we expected that options 1 and 2 would be equally preferred. The unattractive alternative was designed to be 'asymmetrically dominated' such that it was less attractive than either the options 1 or 2, but was similar to option 1 along one attribute (both were held at 30 °C). Importantly, the unattractive phantom, although a poor choice overall, is actually warmer than option 2. We chose these attribute levels because our pilot

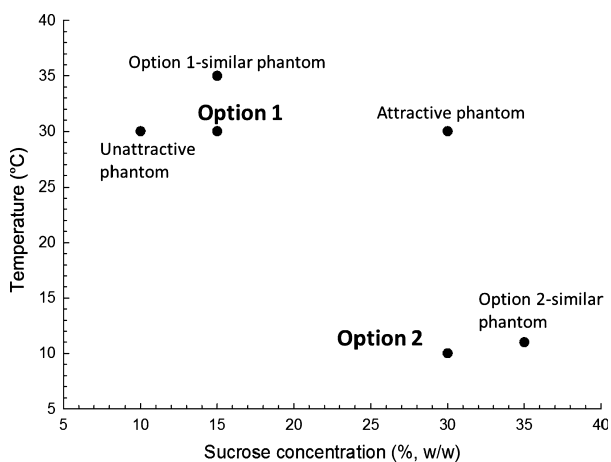


Fig. 1. The attributes of the six feeder types used in our experiments. Ternary choice sets consisted of option 1, option 2 and one of the four phantom types. Note that 'option 2' used in Experiment 2 was held at 11 °C (instead of 10 °C), but is not depicted here for simplicity.

experiments showed that bees were very unlikely to ever revisit an unattractive feeder that was of poorer quality (relative to the other two options) along both attributes. The attractive alternative was substantially more attractive than either option 1 or option 2 along one attribute, and equal on the other attribute. Pilot experiments confirmed that *A. cerana* foragers had the following preference order: attractive feeder > option 1 = option 2 > unattractive feeder.

EXPERIMENT 1A. DO UNATTRACTIVE PHANTOMS INFLUENCE FORAGER PREFERENCES?

Twenty individual bees were presented with either a binary choice set of option 2 (30% sucrose w/w at 10 °C) and option 1 (15% w/w sucrose at 30 °C), or a ternary choice set containing option 1, option 2, and the unattractive phantom (an empty feeder resting on a card that the bees had learned to associate with 10% w/w sucrose at 30 °C). Each individual bee experienced both a ternary and a binary choice set (10 visits in total per set); the order of choice set presentation was randomized.

EXPERIMENT 1B. DO ATTRACTIVE PHANTOM ALTERNATIVES INFLUENCE FORAGER PREFERENCES?

Twenty individual bees were trained and evaluated following the procedure described above, except that the ternary choice set included option 1, option 2, and the attractive phantom (an empty, unheated feeder resting on a card that the bees had learned to associate with 30% w/w at 30 °C). These were new bees that had not previously been used in experiment 1a.

EXPERIMENT 2: DO PHANTOM ALTERNATIVES INCREASE PREFERENCE FOR SIMILAR ITEMS?

We tested the effect of similar phantom items on bee preference by training 20 naïve bees to recognize two feeders: option 1 (15% sucrose held at 30 °C), option 2 (30% sucrose held at 11 °C), an

option 2-similar attractive phantom (35% sucrose held at 11 °C) and an option 1-similar attractive phantom (15% sucrose held at 35 °C) (Fig. 1). The option 1-similar and option 2-similar phantoms were 'range extenders' meaning that they were similar to their target feeder along its worst attribute. Bees were trained using the techniques described above, with the exception that all 20 bees were trained to recognize all four feeder types. During the choice phase, bees were presented with either a binary set (option 1 vs. option 2) or one of two ternary sets [(option 1, option 2, option 1-similar phantom) or (option 1, option 2, option 2-similar phantom)]. Each trained bee was exposed to three choice sets in a random order 10 times.

EXPERIMENT 3: DOES INCREASING THE SIZE OF THE CHOICE SET INFLUENCE HONEYBEE PREFERENCES?

It was possible that changes in bee preference observed in experiments 1 and 2 were caused by the addition of a new item to the choice set, and not by phantom effects *per se*. To control for this possibility, we designed an experiment to test the effect of adding a new, non-phantom item to the choice set. We trained 20 naïve bees to associate a feeder designated as option 1 (15% sucrose held at 30 °C) and a feeder designated option 2 (30% sucrose held at 11 °C) with a particular colour. During the choice phase, each bee encountered either a binary choice set containing option 1 and option 2, or a ternary choice set which contained option 1, option 2 and a novel phantom consisting of an empty, unheated feeder resting on a coloured card that the particular bee had not been trained to recognize. Each bee was exposed to both choice sets in a random order 10 times. If the experimental bees were susceptible to a true phantom alternative effect and not merely to the presence of a novel item in the choice set, then the presence of the novel phantom should not change preference relationships between option 1 and option 2 (Experiment 3), while the true phantoms used in Experiment 2 would result in shifted preference relationships.

STATISTICAL ANALYSES

Group-level preferences

For each experiment, we used a paired *t*-test to test the null hypothesis that the number of forager visits (out of 10) to option 1 did not differ between binary and ternary trials. The experimental unit was the proportion of visits (out of 10) each trained forager made to option 1, so each forager contributed two data points (proportion of visits to option 1 in the binary trials and proportion of visits to option 1 in ternary trials). We used Levene's test to ensure that the assumption of equal variances was met. In Experiment 2, we were interested in determining whether attractive phantoms caused a similarity effect, where the presence of an attractive phantom increases preference for the most similar item – either option 1 or option 2 (Fig. 1). The dependent variable was the number of visits (out of 10) to the focal feeder, where the focal feeder was defined as the feeder (option 2 or option 1) that the attractive phantom was most similar to. Thus, in the option 1-similar trials, the focal feeder was option 1, whereas in the option 2-similar trials, the focal feeder was option 2. We analysed group-level preferences using a mixed model ANOVA, with 'bee ID' included as a random variable, choice set (ternary or binary) as fixed variables and an orthogonal contrast to determine whether the number of visits to the focal feeder in

the ternary trials exceeded the number of visits to the focal feeder in the binary trial.

Individual-level preferences

We tested for individual-level change in preference using a chi-square test. We also determined whether individual foragers had a significant preference for option 1 in the binary and ternary trials using a binomial test with an expected probability of 0.5. We were particularly interested in seeing whether foragers reversed their preferences between options 1 and 2 in the presence of a phantom, as reversal is a particularly dramatic example of a context effect. A forager was classified as having reversed her preferences if she switched from a statistically significant preference for option 1 or option 2 in the binary trials to a significant preference for the alternate feeder type in the ternary trials. In all cases, a significant preference refers to $P < 0.05$.

Results

In general, a trained forager entered the choice arena and hovered briefly above the feeders apparently evaluating the available options before landing. All trained foragers that entered the arena eventually choose one of the options. Foragers never chose more than one feeder per visit. When presented with an attractive phantom alternative, most bees initially approached and landed on the phantom feeder before taking flight and making another selection. The foragers' behaviour suggests that they were unable to ascertain the unrewarding nature of the attractive phantom until they had touched it with their antennae.

To detect a phantom alternative effect experimentally, it is necessary to be certain that the focal animal is aware that an item is unavailable at the time of choice. In several instances, particularly in the unattractive phantom trials, foragers presented with a choice between option 1, option 2 and the phantom did not approach or land on the phantom feeder. As a result, they did not actually experience the 'phantom' condition, and so these bees were omitted from subsequent analysis.

EXPERIMENT 1A: DO UNATTRACTIVE PHANTOM ALTERNATIVES INFLUENCE PREFERENCES?

A total of 7 bees encountered the unattractive phantom and are included in our analysis.

Group-level results

The presence of an unattractive phantom did not have a significant effect on group-level preferences for option 1 ($t_6 = 2.29$, $P = 0.06$).

Individual-level preferences

In the presence of the unattractive phantom, bees changed their preference in favor of option 2, but the extent of preference change was highly heterogeneous among individual bees (Table 1, $P < 0.001$). In the binary trials, three of seven bees had a significant preference with two preferring option 2, and one preferring option 1 (Fig. 2a, < 0.05 , binomial tests). In the ternary trials, five of seven bees had significant preferences with four preferring the option 2, and 1 preferring option 1 (Fig. 2a, < 0.05 , binomial tests). None of the bees made a preference reversal.

EXPERIMENT 1B: DO ATTRACTIVE PHANTOM ALTERNATIVES INFLUENCE FORAGING PREFERENCES?

Thirteen bees encountered the phantom attractive alternative and were included in the analysis.

Group-level preferences

The attractive phantom did not have a significant effect on bees' preferences for option 1 or option 2 ($t_{12} = 1.46$, $P = 0.16$).

Table 1. Chi-square tests of the effects of phantom alternatives on individual-level preferences

	Experiment 1						Experiment 2						Experiment 3		
	Unattractive Phantom ($n = 7$)			Attractive Phantom ($n = 13$)			Option 1-similar Phantom ($n = 19$)			Option 2-similar Phantom ($n = 18$)			Novel Phantom ($n = 20$)		
	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P	χ^2	d.f.	P
Total of χ^2 s	94.6	7	< 0.001	114.4	13	< 0.001	131.1	19	< 0.001	134.5	18	< 0.001	60.47	19	< 0.001
χ^2 of totals	7.3	1	0.007	36.9	1	< 0.001	23.7	1	< 0.001	36.9	1	< 0.001	3.65	1	0.056
Heterogeneity χ^2	87.3	6	< 0.001	103.23	12	< 0.001	107.3	18	< 0.001	103.2	17	< 0.001	56.82	18	< 0.001

We used a chi-square and a chi-square heterogeneity test to examine individual-level changes in honeybee preferences. For each bee, we constructed a 2×2 contingency table that determined whether the proportion of visits (out of 10) to option 1 or option 2 varied between binary and ternary trials using a chi-square test. Overall differences (pooled data across all bees) were compared with a 2×2 contingency table (χ^2 of totals). A significant value (< 0.05) in the χ^2 of totals column indicates that bee preferences in the binary differed from their preferences in the ternary trials in a consistent direction. The difference between the sum of the individual tests (Total of χ^2 s) provides a test of the heterogeneity among bees (heterogeneity χ^2). For more details on the Chi-square heterogeneity test, please see Sokal & Rohlf (1995).

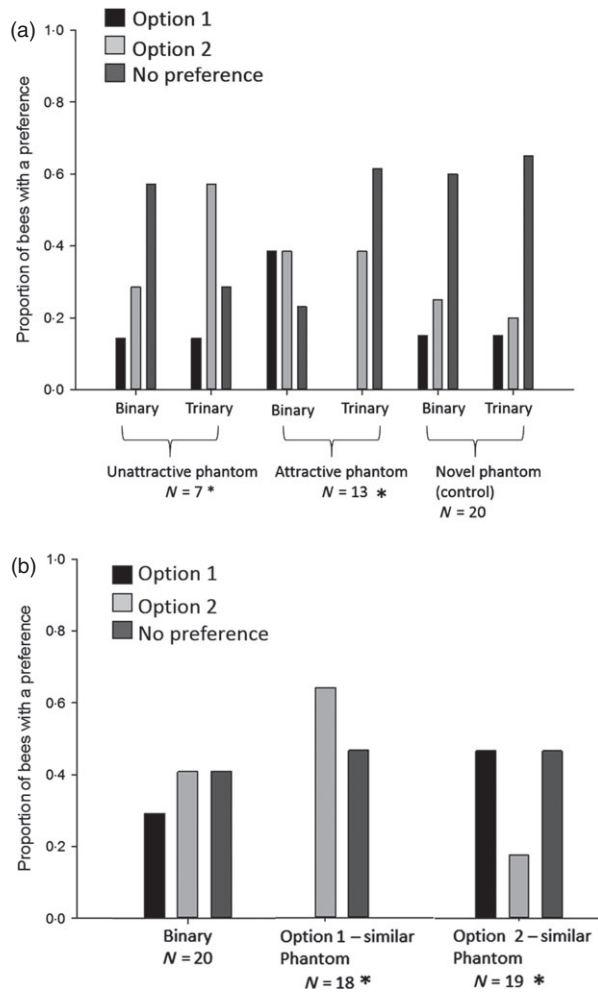


Fig. 2. Preferences of foraging bees for option 1 and option 2 feeders in the presence (ternary choice) and absence (binary choice) of phantom decoy feeders. Bees were said to ‘prefer’ a feeder type if they made a significantly greater number of visits to that feeder (binomial test, expected preference = 0.5). Bees that did not have a significant preference ($P > 0.05$) were coded as ‘no preference’. (a) Experiments 1 and 4: unattractive and attractive phantoms (that had been previously experienced by test bees) and novel phantom decoys. (b) Experiment 2. Preferences of foraging bees for option 1 and option 2 feeders in the presence of option 1-similar and option 2-similar phantoms. The asterisk denotes a significant preference for option 2 in the presence of an option 2-similar phantom.

Individual-level preferences

The presence of the attractive phantom caused bees to change their preference in favour of option 2, but the extent of preference change was heterogeneous among individual bees (Table 1, $P < 0.001$). In the binary trials, 10 of 13 bees had significant feeder preferences with 5 preferring option 1 and 5 preferring option 2 (Fig. 2a, binomial tests, $P < 0.05$). In the ternary trials, 5 of 13 bees had a significant feeder preference, all of which were in favour of option 2 (Fig. 2a, binomial tests, $P < 0.05$). Three bees made preference reversals from option 1 to option 2.

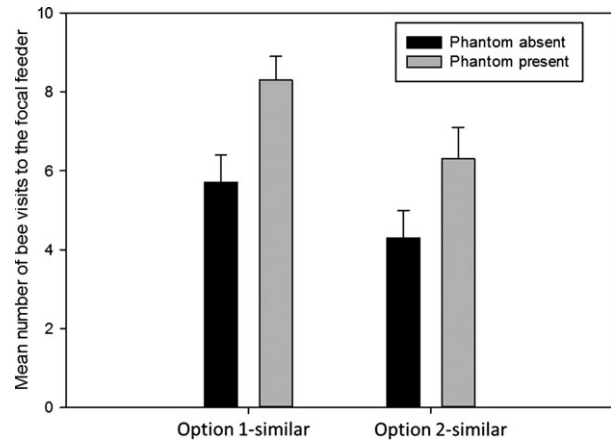


Fig. 3. Experiment 2. The effect of option 1-similar and option 2-similar phantom alternatives on bee preferences. Across option 2-similar and option 1-similar trials, foragers significantly changed their preference to the feeder that was more similar to the phantom ($P = 0.012$, see main text). Error bars are standard errors of the mean.

EXPERIMENT 2: DO PHANTOM ALTERNATIVES INCREASE PREFERENCE FOR SIMILAR ITEMS?

In our option 1-similar trials, 19 of 20 bees experienced the phantom feeder and were included in the analysis; in the option 2-similar trials, 18 of 20 bees were included in the analysis.

Group-level preferences

The presence of a phantom significantly changed the bees’ preferences between option 1 and option 2 such that there was a significant effect of treatment (binary/ternary) on bee preference (Fig. 3, ANOVA $F_{2,35} = 4.44$, $P = 0.019$). In trials with the phantom present, foragers significantly changed their number of visits towards the focal feeder (the one that was most similar to the phantom) relative to their preference in the binary trial (Fig. 3, orthogonal contrast $F_{1,35} = 5.6$, one-tailed $P = 0.011$). Overall there were no significant differences between the preferences of individual bees for option 1 and option 2 ($F_{19,35} = 1.23$, $P = 0.29$).

Individual-level preferences

In general, individual bees changed their preference towards the focal feeder in the presence of option 2-similar and option 1-similar phantoms (Fig. 2b, Table 1). In the binary trials, 12 of 20 bees had significant preferences, with 7 bees preferring option 2 and 5 bees preferring option 1 (Fig. 3 binomial tests, $P < 0.05$). When the option 1-similar phantom was present, 11 of 18 bees had significant feeder preferences – all in favour of option 1 (Fig. 3, binomial tests, $P < 0.05$). Two bees made preference reversals in favour of option 2. When the option 2-similar phantom was added to the choice set, 8 of 19 bees

preferred option 2 and 3 of 19 bees preferred option 1 (Fig. 2b, binomial tests, all $P < 0.05$). Two bees made preference reversals. One changed from preference for option 1 to preference for option 2, and the second changed from option 2 to option 1.

EXPERIMENT 3: EFFECT OF A NOVEL PHANTOM

Group-level preferences

The presence of a novel phantom feeder had no effect on bee preferences ($t_{19} = 1.12$, $P = 0.27$).

Individual-level preferences

Individual bees did not change their preferences in the presence of novel phantoms (Table 1, $P = 0.056$). In the binary trials, 8 of 20 bees had significant feeder preferences, with 5 preferring option 2 and three preferring option 1 (Fig. 2b, binomial tests, $P < 0.05$). In the ternary trials, 4 of 20 bees preferred option 2 and 3 of 20 preferred option 1 (Fig. 2b, binomial tests, $P < 0.05$). A single bee reversed her preference in favour of option 2.

Discussion

Like humans lured in by items later revealed to be sold out, honeybees alter their preferences when an unavailable item is added to their choice set. Although we did not detect significant preference shifts in either the attractive or unattractive decoys at the group level (Experiment 1), we did find significant preference shifts at the individual level when bees encountered an attractive phantom decoys. Our results suggest that, as in humans, the phantom decoy effect occurs when bees are confronted with an attractive phantom alternative. In the presence of an attractive phantom, bee preferences shifted from a 50 of 50 split between option 1 and option 2 during the binary trials to a 100% preference for option 2 after experiencing the attractive phantom (Fig. 2a). This change in preference included 3 bees that showed statistically significant preference reversals from option 1 to option 2. In contrast, no bees experienced a preference reversal after encountering an unattractive phantom. Our individual-level analyses found weak evidence that the unattractive phantom altered preferences in favour of option 2 (Table 1). While our results seem to indicate that unattractive phantoms are weakly effective at causing preference shifts, it is important to note that our interpretation is hampered by low sample size in the unattractive phantom trials. Low sample size was due to the fact that, unsurprisingly, very few bees actually selected (and therefore experienced) the unattractive phantom feeder.

We found evidence for a similarity effect in both our individual- and group-level analyses (Experiment 2), where phantoms tended to increase preference for the

available alternative most similar to the phantom (Fig. 3). Along with previous studies on humans and cats (Pettibone and Wedell 2007, Scarpi 2011), our results support the idea that phantom alternatives result in increased preference for similar items in foraging animals. The cognitive mechanisms underlying the similarity effect in bees are currently unknown. We suggest that encountering a phantom causes bees to change the way they prioritize either warmth or concentration, so that encountering a high quality warm feeder results in a preference for warmer feeders, while contact with a high sugar-concentration feeder causes an increased preference for sugary feeders. Thus, contact with a phantom primes bees to prefer items with similar characteristics.

Our key result, that encountering an attractive phantom increases forager preference for similar items, is mirrored by experimental findings in bumblebees (Gigord *et al.* 2002). In an experiment designed to test floral mimicry in unrewarding orchids, Gigord *et al.* (2002) trained bees to forage on feeder arrays containing one rewarding 'model' species and two non-rewarding mimics that differed in corolla colour. When the rewarding 'model' flower was removed from the array (leaving the two unrewarding mimic species), bees preferentially landed on the non-rewarding flower that most closely matched the corolla colour of the unavailable rewarding flower. Although the experiment was not designed to test phantom alternatives effects, the removal of the rewarding flower mimics a phantom alternative, as bees would have entered the array with the expectation of encountering a rewarding flower. Gigord *et al.*'s (2002) experiment is particularly interesting because it used real flowers, rather than artificial feeders. Our combined results strongly suggest that the phantom alternative effect is a real phenomenon that alters the preferences of foraging bees.

Phantom alternatives are, by definition, unattainable: Why, then, do they influence choice? The presence of a phantom alternative may give the decision-maker information about the availability of resources in the environment. For human consumers, the presence of sold out items may signal that an item is in high demand; this induces a feeling of urgency such that individuals will be more likely to quickly purchase remaining items, a phenomena termed the 'immediacy effect' (Ge, Messinger & Li 2009). The immediacy effect can cause preference reversals if individuals use different strategies for making fast decisions than they do when free from time pressure. Phantom alternatives can also provide vicarious 'social information' about the desirability or quality of an item. If an item is sold out, the consumer may perceive that similar items must also be of high quality (called 'an informational cascades effect') (Pratkanis & Farquhar 1992). For honeybees, empty flowers could signal either that a particular flower is in high demand and therefore attractive (an informational cascades effect), or that flowers in general are in demand necessitating a rapid

response (an immediacy effect). In both cases, phantoms are included in the decision-making process because they provide useful information.

Alternatively, the initial inclusion of phantoms in the choice set may change preferences by altering the heuristics employed by the forager to make choices. For example, mathematical models of decision-making suggest that context effects in general result from constraints on biological information processing and can arise whenever a decision-making system is based on positive feedback (Nicolis *et al.* 2011). Positive feedback occurs whenever a change in a system is self-reinforcing (Camazine *et al.* 2003) and is thought to be the mechanism behind decision-making processes in brains (Deco, Rolls & Romo 2009). According to the Nicolis *et al.* (2011) model, simply changing the number of items under consideration can alter expressed preferences. Our result is not solely explained by increased choice set size, as adding a novel phantom (our control experiment) had no impact on bee preferences. Nevertheless, the Nicolis *et al.* (2011) model could still apply to our results, if, for example, novel feeders result in lower positive feedback than known feeders. Whether phantom alternatives alter preferences by providing the forager with information or by altering choice heuristics is an open question that will likely require additional modelling and empirical study.

Two types of phantom alternatives have been described in the literature (Pratkanis & Farquhar 1992). Unknown phantoms, like the ones used in our experiment, occur when the decision-maker does not realize an item is unavailable until they try to access it. 'Known phantoms' constitute the second, less studied, type of phantom alternative. Known phantoms are those in which the decision-maker is aware that an item is unavailable from the beginning of the decision-making process (Pratkanis & Farquhar 1992). Examples include properties on real estate boards that are labelled 'sold', attractive but married people and forbidden items like alcohol for children. Several studies have shown that known phantoms can influence human preferences (reviewed in Pratkanis & Farquhar 1992). In honeybees, closed but otherwise rewarding flowers may constitute known phantoms because the bee is aware that a flower is unlikely to have nectar at certain times of the day. Most flowers are only open (and therefore available) for part of the day, and a number of studies have found that honeybees are very good at remembering when each flower type is typically open (e.g. Gallistel 1989). Our research has shown that unknown phantoms can influence foraging behaviour in honeybees; whether the same is true for known phantoms is an open question.

Our results open the possibility that nectarless flowers may have far reaching effects on the dynamics of plant–insect interactions, community composition and competitive interactions between pollinators. Over time, pollinators are expected to learn to avoid non-rewarding

species by switching to alternative species (Smithson & Gigord 2003). If our results hold under field conditions, then we predict that pollinators that encounter an empty flower will be less likely to switch to flower species that share the characteristics of the non-rewarding species. Given that an increase in pollinator visits tends to result in higher seed set, our results open up the possibility that by shifting pollinator preferences, empty flowers could have otherwise-unpredicted influences on community composition. For example, Molina-Montenegro, Badano & Cavieres (2008) found that highly rewarding invasive species can act as pollinator 'magnets' for less attractive plants, resulting in increased seed set for the less attractive species. If magnet species also have empty flowers (either because they have been previously emptied by other insects, or because the plant regularly produces nectarless flowers), then the presence of the 'magnet' species could potentially shift preference relationships among the remaining flowers in the community, thereby altering their reproductive success and ultimately changing the species composition of the floral community.

Unfortunately, no studies to date have tracked the choice behaviour of foragers after they abandon an empty flower in the wild, likely because this would be logistically difficult under field conditions. While tracking the flower choices of small pollinators like bees is probably infeasible (at least with current tracking technologies), it might be possible to track the choices of larger nectivores such as birds and bats. It will be interesting to determine the extent to which phantom alternative effects influence pollinator preferences in natural environments.

A growing number of studies on humans (Huber, Payne & Puto 1982; Huber & Puto 1983; Tversky & Simonson 1993; Bateson, Healy & Hurly 2002), birds (Hurly & Oseen 1999; Bateson 2002; Shafir, Waite & Smith 2002; Morgan *et al.* 2012), insects (Shafir, Waite & Smith 2002) and a unicellular slime mould (Latty & Beekman 2011) have established that increasing the choice set by adding a new item, even one that is clearly inferior to the original options, can change the decision-maker's preferences. Like Bateson (2004) we suggest that the existence of these 'context effects' highlights the need to be very careful in the way preference tests are constructed and interpreted. Our experiments provide an even stronger caution, since we have shown that decoy alternatives can influence choice even if they are not currently available. This is particularly relevant for honeybees and other nectar feeders that may have to choose among choice sets containing many different flowers in many different combinations, some of which may be unrewarding. Phantom alternatives could also influence other decision-making domains such as in mate choice and nest site selection. The existence of phantom alternative effects may therefore have widespread implications for our understanding of animal decision-making in natural environments.

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Data accessibility

All supporting data files for this publication have been deposited in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.vm62n> (Tan *et al.* 2014a).

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