PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

Cite this article: Hemingway CT, DeVore JE, Muth F. 2024 Economic foraging in a floral marketplace: asymmetrically dominated decoy effects in bumblebees. *Proc. R. Soc. B* **291**: 20240843.
https://doi.org/10.1098/rspb.2024.0843

Received: 12 April 2024
Accepted: 16 August 2024

Subject Category:
Behaviour

Subject Areas:
behaviour, cognition, ecology

Keywords:
Bombus impatiens, decoy effects, nectar concentration, reward rate, value perception

Author for correspondence:
Claire T. Hemingway
e-mail: chemingw@utk.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.7441750.

THE ROYAL SOCIETY
PUBLISHING

Economic foraging in a floral marketplace: asymmetrically dominated decoy effects in bumblebees

Claire T. Hemingway[1,2,3], Jennie E. DeVore[3] and Felicity Muth[3,4]

[1]Department of Ecology & Evolutionary Biology, University of Tennessee, Dabney Hall, 1416 Circle Drive, Knoxville, TN 37996, USA
[2]Department of Psychology, University of Tennessee, Austin Peay, 1404 Circle Drive, Knoxville, TN 37996, USA
[3]Department of Integrative Biology, University of Texas at Austin, 2415 Speedway, Austin, TX 78712, USA
[4]Department of Neurobiology, Physiology, and Behavior, University of California,196 Briggs Hall, Davis, CA 95616, USA

CTH, 0000-0002-0901-1553; JEDV, 0000-0003-2261-7987; FM, 0000-0003-0904-0589

While most models of decision-making assume that individuals assign options absolute values, animals often assess options comparatively, violating principles of economic rationality. Such 'irrational' preferences are especially common when two rewards vary along multiple dimensions of quality and a third, 'decoy' option is available. Bumblebees are models of decision-making, yet whether they are subject to decoy effects is unknown. We addressed this question using bumblebees (*Bombus impatiens*) choosing between flowers that varied in their nectar concentration and reward rate. We first gave bees a choice between two flower types, one higher in concentration and the other higher in reward rate. Bees were then given a choice between these flowers and either a 'concentration' or 'rate' decoy, designed to be asymmetrically dominated on each axis. The rate decoy increased bees' preference in the expected direction, while the concentration decoy did not. In a second experiment, we manipulated choices along two single reward dimensions to test whether this discrepancy was explained by differences in how concentration versus reward rate were evaluated. We found that low-concentration decoys increased bees' preference for the medium option as predicted, whereas low-rate decoys had no effect. Our results suggest that both low- and high-value flowers can influence pollinator preferences in ways previously unconsidered.

1. Introduction

Animals face a myriad of decisions in their daily lives, and central to decision-making is the ability to assess the potential benefits (or rewards) associated with different options. Classic economic models such as expected utility theory (for humans) [1] and foraging theory (for non-human animals) [2–5] assume that an objective measure of value is determined for each option through combining several attributes of value, often related to fitness [6,7]. However, a multitude of studies in human [8–10] and non-human [11–13] animals have shown that a reward's value is rarely absolute, but instead is perceived relative to expectations based on experience with similar rewards or other available options. This can lead to economically 'irrational' decisions [14], where the magnitude and even the direction of preferences depend on the composition of the choice set. For instance, many animals expecting a high-quality reward are more likely to reject a medium-quality reward than individuals expecting a low-quality one (e.g. honeybees [15], ants [16], pigeons, rats [17]). When faced with two or more choices, animals often make decisions relative to the other options available, which can lead to circular preferences where no one option is 'best' (honeybees [18], grey jays [19]). While considered to be economically irrational, such behaviours can still be ecologically rational [20] through allowing animals to more efficiently exploit environments that vary in time and space [21]. Throughout this paper, we refer to 'irrational' in terms of economic rationality.

Decoy effects are a common example of context-dependent preferences in which the introduction of an apparently 'irrelevant' option into a choice set alters preferences between two or more preferred options. Decoy effects are typically encountered in 'unfriendly' choice environments where options have two or more value dimensions (e.g. price and quality) [22] that can be directly compared. When choosing between one option, the 'target', which is superior in one dimension but inferior in another (e.g. 'R' on figure 1), and a second option, the 'competitor' (e.g. 'C' on figure 1), preference between these two options can be shifted by the addition of a third option, the 'decoy' [10] (e.g. D_R on figure 1). The decoy creates an asymmetric dominance, being worse than the target along both dimensions, but only worse than the competitor along one, making the target appear relatively better. For instance, when choosing between a five-star restaurant 25 min away, and a three-star restaurant 5 min away, people would be more likely to drive to the five-star restaurant when a decoy is added: a four-star restaurant 35 min away. The five-star restaurant is both higher quality and closer than the four-star restaurant, whereas the three-star restaurant is only closer (i.e. it is asymmetrically dominated). Such effects are common in humans and marketers frequently manipulate the decision context to steer consumers towards particular options (e.g. [23,24]).

Outside of humans, decoy effects have been widely documented across a diverse array of taxa, including slime moulds, insects, birds, frogs and mammals (reviewed in [14,25]). There is considerable variation between species in the presence and magnitude of these biases. For example, frog-eating bats make rational choices in the presence of an acoustic decoy [25] but fruit-eating bats show preference shifts when choosing between different fruits [26]. Even within species, there is evidence that different reward dimensions are evaluated using different decision rules [27]. For example, hummingbirds show context-dependent preferences for nectar concentration and volume but not corolla length [11,27,28]. Such findings suggest that, while common, comparative evaluation is not a general feature of decision-making in animals, but instead may represent an adaptive solution to ecological pressures surrounding decisions in the wild [21].

Generalist pollinators, such as honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.), are classic systems for the study of foraging economics, with foragers encountering a 'floral marketplace' [29,30]. Previous work indicates that bees largely perceive the value of nectar in relative terms. For example, honeybees show both decoy effects [31,32] and circular preferences [18]. Relative value perception may represent a general feature of decision-making in nectarivores [21], which feed on tightly clumped, ephemeral resources, allowing for rapid sampling and comparison of flower types [21]. On the other hand, floral rewards vary along several dimensions of value [13,33], and such evaluation mechanisms may depend on the attributes evaluated. However, studies of floral preferences rarely explore how decision-making may vary across different dimensions of quality (but see [11,13]).

Here we investigated decoy effects in bumblebees concerning two aspects of nectar quality shown to be important in foraging decisions: sugar concentration and reward rate. Sugar concentration is one of the most important aspects of nectar quality that bumblebees attend to, with nectar sugars providing the main source of energy for flight [34]. Bees and other pollinators generally prefer higher sucrose concentrations [15,35] and plants often compete along this reward axis [36,37]. The presence of nectar in flowers (reward rate) can also vary considerably within and between flower types due to daily patterns of reward depletion and renewal (e.g. [38]). Bees attend to nectar's replenish rate, leaving patches sooner when the frequency of rewarding flowers falls below a certain threshold (e.g. [39]) or preferentially avoiding certain flower types (e.g. [40,41]). To assess how bumblebees evaluate these attributes together and separately, we conducted two experiments. In the first experiment, we asked whether the addition of decoy flowers would shift bees' preferences between two preferred flowers. Bees were given a binary choice between two artificial flower types, one higher in concentration and the other higher in reward rate (figure 1). They were then given a trinary choice between these two flowers and either a 'concentration decoy' (D_C), which was asymmetrically dominated by a high-concentration flower, or a 'rate decoy' (D_R), dominated by a high-rate flower. If decoy flowers shift bees' preferences, we predicted this would increase preferences for target flower types (table 1).

After finding D_R induced the predicted effect, but D_C did not affect bees' relative preferences between flowers, we conducted a second experiment to explore this further. Specifically, we asked whether bees use comparative evaluation to a greater degree when assessing nectar concentration than reward rate. This could explain why D_R, which was low in concentration, increased the preference for R, while the same was not true for D_C. Specifically, if bees in Experiment 1 are primarily shifting preferences in response to comparative evaluation with a low-value concentration option, we would expect the lower concentration D_R to increase the preference for R (R now appears better compared with D_R), while D_C may not have an equivalent effect if bees do not value rate comparatively. To test this hypothesis, we gave bees a choice between medium- and high-quality flowers on a single dimension (concentration or reward rate), followed by the addition of a low-quality decoy. If bees use comparative evaluation to a greater degree with concentration, then the addition of a low-quality option would increase bees' relative preference for the medium-quality option on the concentration, but not reward rate, axis.

2. Material and methods

(a) Study system

We conducted experiments with bumblebees (*Bombus impatiens*) ($n = 103$) from commercially reared queenright colonies ($n = 8$) (Koppert, USA); sample sizes per colony are shown in electronic supplementary material, table S1. Colonies were maintained

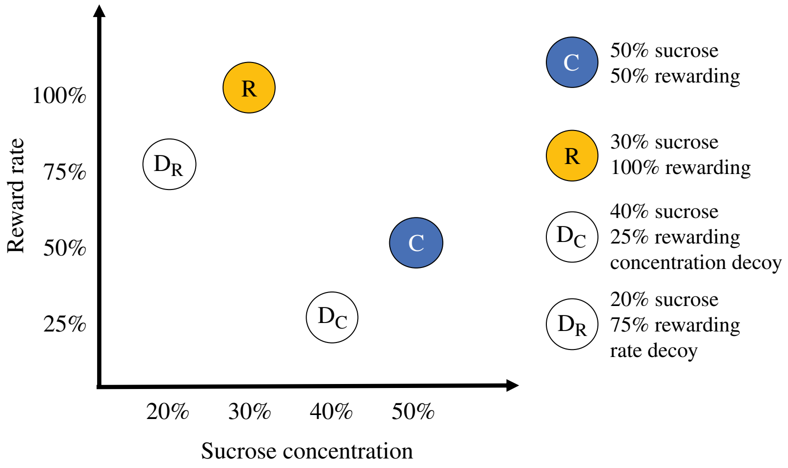

Figure 1. Artificial flowers and rewards used in Experiment 1. Flower C was high in concentration and intermediate in reward rate. Flower R was high in reward rate and intermediate in concentration. The rate decoy (D_R) flower had a higher reward rate than flower C but was less rewarding than flower R on both axes. The concentration decoy (D_C) flower had a higher concentration than flower R was less rewarding than flower C on both axes.

Table 1. Asymmetric dominance relationship between decoy flowers and main flower types, C and R, in Experiment 1, and predictions of the asymmetrically dominated decoy effect. Flower C is high in concentration (50% w/w) and intermediate in reward rate (50% rewarding). Flower R is high in reward rate (100% rewarding) and intermediate in concentration (30% w/w). Flowers D_R (20% sucrose, 75% rewarding) and D_C (40% sucrose, 25% rewarding) were designed to be asymmetrically dominated by flowers R and C, respectively.

	relationship to flower R	relationship to flower C	prediction of asymmetrically dominated decoy effect
D_C: concentration decoy	**R** is superior to decoy on rate axis but not concentration axis	**C** is superior to decoy on both axes	decoy will increase preference for option **C**
D_R: rate decoy	**R** is superior to decoy on both axes	**C** is superior to decoy on concentration axis but not rate axis	decoy will increase preference for option **R**

in small boxes (approx. 40 cm^3) on 30% (w/w) sucrose solution and honeybee-collected pollen (approx. 0.5 g/day, Koppert Biological Systems, USA). We connected colonies sequentially to a flight arena ($l \times w \times h$: 122 × 61 × 61 cm), using a clear plastic tube with sliding doors to control the entry and exit of bees into the arena. The floor of the flight arena was lined with green laminate and the sides and top consisted of black mesh screens. The arena was lit from above by a 40 W LED light placed atop the arena and the room was illuminated with fluorescent light on a 12/12 h light/dark schedule.

(b) Experimental arrays and floral stimuli

The vertical arrays used for experiments consisted of black corrugated plastic sheets with 24 holes for ‘flowers’ arranged in a 6 × 4 grid. Twelve artificial flowers were pseudorandomly arranged to be equally represented across the array, with unoccupied holes sealed using black rubber bungs (figure 2*a*). We constructed artificial flowers from 1.5 ml plastic Eppendorf tubes with small holes cut in the base of the tubes to pipette sucrose solution (figure 2*a*). The ‘corollas’ of these artificial flowers were made from laminated, coloured circular discs (5 cm in diameter) placed around the opening of the tube. We used three colour stimuli to correspond to our three flower types: blue, yellow and white (figures 1 and 2*a*).

To accurately monitor and manipulate the reward rate of flowers (see §d below), we attached rotating paper discs to the back of our artificial flowers, which corresponded to the four rates of reinforcement used across both experiments (electronic supplementary material, figure S1). There were eight positions on the discs that were either marked with an ‘X’ or marked with the sucrose concentration used for that flower type (e.g. 50%). The spot in the upright position denoted whether a flower was empty or full, and whether to refill the flower following a bee visit. The experimenter rotated the disc a single position each time a bee visited the flower, only refilling it on positions not marked by ‘X’. Discs were only visible to the experimenter and not to the foraging bee.

(c) Initial training

During the initial training phase, we first allowed bees to forage for sucrose in the foraging arena by giving a whole colony access to a white-wicked feeder containing 30% (w/w) sucrose solution. This was a single plastic container filled with sucrose solution that had an immersed and saturated wick (a braided dental cotton roll, Richmond Dental, USA) protruding vertically from the lid, on which bees could land and drink from. We initially placed the feeder close to where foragers exited their colony. Over 1–2 days, we incrementally moved the feeder towards the end of the arena until bees readily foraged on it and

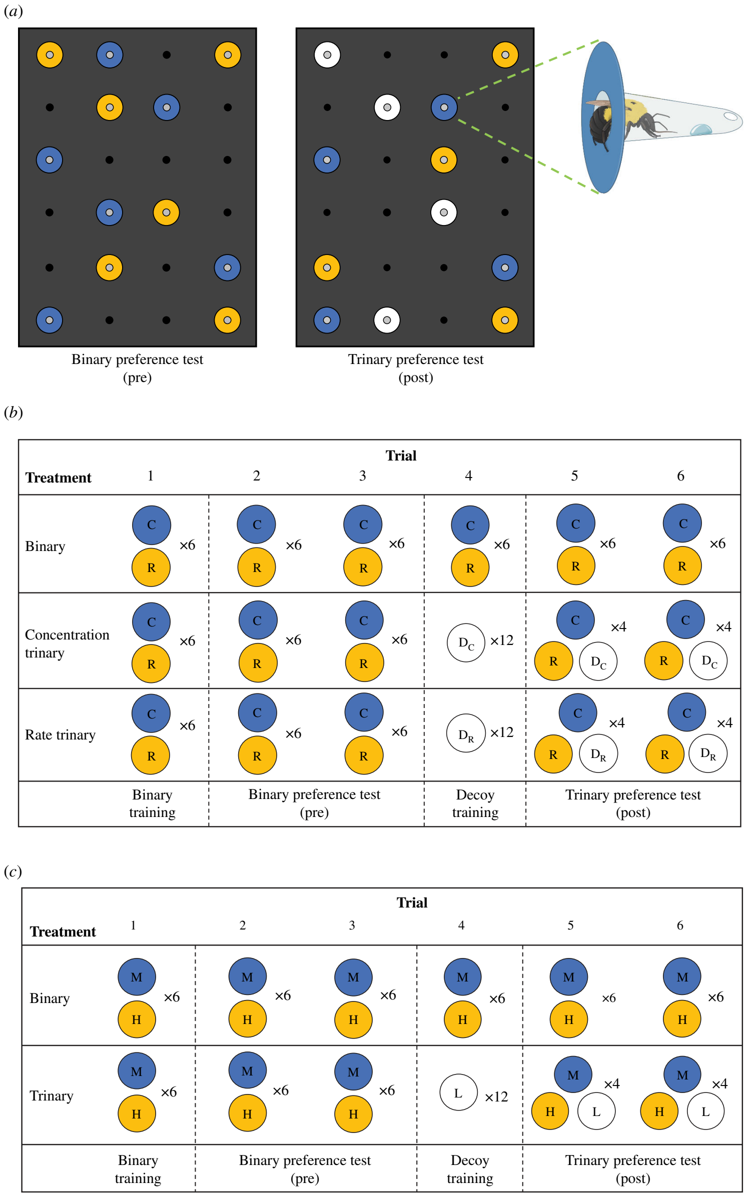

Figure 2. (*a*) Vertical floral arrays used for training and testing in both experiments. Array for the binary (pre) test trials are shown on the left and trinary (post) test trials on the right. (*b*) Overview of Experiment 1. Bees in all treatments experienced six trials; for flower reward values, see figure 1. The binary group experienced two choices (R and C) across six trials, while trinary groups experienced only decoy flowers on trial 4, followed by three choices (R, C and D) on trials 5 and 6. Each trial had 12 flowers total, and numbers next to flowers represent the number of flowers of each flower colour present on that trial. (*c*) Overview of Experiment 2. Bees in the binary treatment were given the same choice across six trials between medium (M) and high (H) flowers. Bees in the trinary treatment were given a 'decoy' trial on trial 4 where they had access to low (L) flowers only, followed by a trinary choice on trials 5 and 6.

returned to the colony. We then trained bees to visit artificial flowers on a 24-flower array similar to the experimental array with the exception that no colour stimuli were used (Eppendorf tubes alone). All flowers were provisioned with 30% (w/w) sucrose solution. During this initial training, flowers contained an additional hole on top which we used to mark individual bees' thoraces using non-toxic, water-based paint markers (POSCA, USA). Bees were each given a unique colour combination for identification. Foragers consistently leaving the colony to forage from this array (three or more visits) were selected for use in experiments.

(d) Experimental protocol

(i) General protocol

Each bee was assigned to one of either three (Experiment 1) or four (Experiment 2) treatments. All treatments were represented across all colonies within each experiment (electronic supplementary material, table S1). We systematically varied treatment order across bees within a given colony to avoid any temporal confounds. All bees experienced a total of six consecutive training and testing trials (Experiment 1: figure 2*b*; Experiment 2: figure 2*c*). Trials lasted around 10 min each with bees making approximately 20–30 flower choices per trial. Twelve flowers were used on the array during the training and testing trials, and individual flowers could be re-visited since they were either re-filled or left empty. For all experiments, a flower 'choice' was defined as a bee entering a flower and extending her proboscis. Flowers varied in concentration (20%, 30%, 40% and 50%

sucrose (w/w)) and reward rate (25%, 50%, 75% and 100% rewarding). Reward volumes were kept constant at 4 µl per flower. We used three different flower colours: blue, yellow and white to indicate the different flower types. Blue and yellow flowers were always used as the two main flower types for each experiment, while decoy flowers were always white (figure 2, electronic supplementary material, figure S4). We chose this design since a previous study indicated that bees did not show a strong preference between this particular blue and yellow (for chromatic contrast, see [42]). Reward values were chosen such that bees had roughly equal preferences between the two main flower types and were consistent with previous studies demonstrating robust preferences in bees for higher nectar concentrations and rates of reinforcement [15,35,43]. The energy content of both flower types, as well as the two decoy flowers, is shown in electronic supplementary material, table S2.

In both experiments, each bee was given the following trials (figure 2*b*,*c*): **Trial 1: binary training:** bees were given a choice between six blue and six yellow flowers; this trial allowed bees to gain experience with the two main flower types. **Trials 2 and 3: binary preference tests:** these trials allowed us to assess bees' preference between the two main flower types. **Trial 4: decoy training**: bees in trinary treatments received a trial with only decoy flowers to ensure that all bees gained experience with the decoy before the trinary preference trials; bees had to visit a minimum of 10 decoy flowers to move on to the next trial. In place of the decoy training trial, bees in the binary treatment received another trial with the initial two flower types. We did this rather than a 'blank' trial to ensure that foragers did not lose foraging motivation and to give bees across treatments the same number of trials overall. **Trials 5 and 6: trinary preference test:** bees in binary groups were given the same choice again, while bees in trinary groups had the original two flowers alongside the decoy option. These final two trials allowed us to compare bees' binary versus trinary preferences both within and across treatments. Bees were not trained to the decoy until trial 4, as prior experience with decoy flowers may have influenced bees' initial preferences for R versus C, even if those flower types were absent during later choice tests [32]. All trials were recorded using a Canon camcorder on a tripod placed near the nest box and facing the array.

Experiment 1: are bumblebees subject to decoy effects?

We tested 55 bees from five colonies (electronic supplementary material, table S1). Bees were trained and tested individually in one of three experimental treatments: a binary choice between two flowers, one higher in reward rate (flower R, yellow) and the other higher in concentration (flower C, blue), or one of two trinary choice treatments where they also had a decoy flower (either D_R or D_C). Flowers R (30% sucrose, 100% rewarding) and C (50% sucrose, 50% rewarding) were designed to be roughly equally preferred, with each option being superior to the other on one dimension (figure 1). Flowers D_R (20% sucrose, 75% rewarding) and D_C (40% sucrose, 25% rewarding) were designed to be asymmetrically dominated by flowers R and C, respectively (figure 1, table 1).

Experiment 2: how do bumblebees evaluate reward rate and concentration dimensions separately?

After finding in Experiment 1 that D_R induced the predicted effect, but that D_C did not affect bees' relative preferences between flowers (see §3), we conducted a second experiment to better understand this result. In Experiment 2, we tested how bees evaluate each reward dimension (concentration and reward rate) separately by determining how the relative preference between a medium and high option was affected by the presence of a lower (decoy) option. We tested 48 bees from three colonies (electronic supplementary material, table S1). Using a similar design to Experiment 1, bees were trained and tested individually across one of two experimental treatments (binary or trinary) for each reward dimension (figure 2*b*). Bees in binary treatments were given a choice between a medium-quality flower (flower M) and a high-quality flower (flower H) (figure 3). Bees in trinary treatments were also given experience with a low-quality decoy flower (flower L) and subsequently given a three-choice test between all three flower types (figure 2*b*). In this experiment, because there was a clear ranking of flowers within each choice set, any initial colour preference would likely be enhanced by the preference for the higher quality flower. As such, we counterbalanced colour (blue or yellow) across the two flower types (flowers M and H) to control for any colour bias associated with the best option.

(e) Data analysis

(i) Preference measures

We tested whether bees shifted preferences within treatments between the pre-test trials (2 and 3) and the post-test trials (5 and 6), and if this varied across treatments. In both experiments, we addressed preference shifts both in terms of changes to *relative preference* and changes to *absolute preference,* as two different measures of economic rationality. *Relative preference* is defined as the proportion of choices for one of the main flower types out of the total number of choices for both flower types. Changes in relative preferences are a violation of the 'constant-ratio rule', which requires that the relative preference between pre-existing options remains stable when an inferior option is added to a choice set. For Experiment 1, this was $R/(R+C)$; for Experiment 2 this was $M/(M+H)$. In contrast, *absolute preferences* are the proportion of choices for each flower type out of the total number of choices for all options, including the decoys. Changes in absolute preference are a violation of 'regularity' which states that the proportion of choices for an option should not increase when the choice set is enlarged [44]. Unlike relative preference, absolute preferences for either flower type could vary independently of one another, so we include this measure for both flower types. In Experiment 1, we measured the absolute preference for R ($R/(R+C+D)$) and C ($C/(R+C+D)$). In Experiment 2, absolute preference for flower M was: $M/(M+H+L)$, and for flower H was: $H/(H+M+L)$.

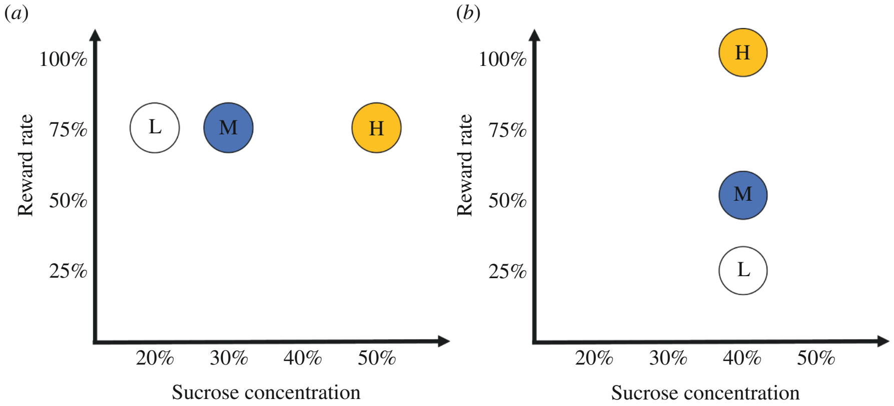

Figure 3. Artificial flowers and rewards used in the two treatments in Experiment 2. (*a*) Rewards varied along the concentration dimension but were equal in reward rate (all flowers 75% rewarding). High-reward flowers (H) had 50% sucrose (w/w), medium-reward flowers (M) had 30% sucrose and low-reward flowers (L) had 20% sucrose. (*b*) Rewards varied along the rate dimension but were equal in concentration (40% sucrose). High-reward flowers (H) were rewarded 100% of the time, medium-reward flowers (M) were rewarded 50% of the time and low-reward flowers (L) were rewarded 25% of the time. Flower colour (yellow or blue) was counterbalanced across M and H flowers in both treatments.

(ii) General data analysis

We conducted all analyses in R (v. 4.2.3) [45]. Models were conducted using the glmer() function in the lme4 package [46]. We ran models with interaction terms as described below, evaluating fits using the anova() function in the car package [47] and excluding non-significant interactions in a step-wise manner. For all binomial logistic regressions, we tested for overdispersion and met model assumptions (ratio of residual deviance to degrees of freedom > 1). Where we found interactions, we used the function and package ‘emmeans’ [48] for *post hoc* comparisons (Tukey’s honestly significant difference (HSD) tests). Data and analyses are published in the Dryad Digital Repository [49].

(iii) Experiment 1

To assess whether bees shifted their *relative preference* from the binary to trinary test phase, and if this effect varied across treatments, we ran binomial generalized linear mixed effect models (GLMMs). To do this, we included choices for the two main flower types as a binary response (choice for C = 0; choice for R = 1). We tested for an interaction between ‘treatment’ (binary, concentration trinary, or rate trinary) and ‘test type’ (binary (pre) or trinary (post) preference tests). We included ‘bee’ and ‘colony’ as random intercepts.

To assess if bees shifted their *absolute preference* for the target flower, we ran two separate binomial GLMMs with choices for the two main flower types (R or C) as the response variable. The focal flower was coded as 1 and all other choices as 0, using the same explanatory variables and interaction term as for the relative preference analysis.

To determine if the two trinary treatments differed in their experience with the decoy in the fourth trial (decoy training trial), we ran a linear mixed effect model (LMM) with number of visits to the decoy as the response variable, trinary treatment as the main effect, and colony included as a random effect. In addition, to determine if experience with the decoy affected preference shifts, we asked whether the number of visits to the decoy flowers in the fourth trial influenced the magnitude of preference shift between the pre- and the post-choice tests. To do this, we conducted a GLMM for each trinary treatment group separately. The relative preference for flower R was the response variable and we tested for an interaction between number of visits to the decoy in the fourth trial (continuous variable) and test type (pre or post). We included ‘bee’ as a random intercept but could not include ‘colony’ due to a singularity issue.

(iv) Experiment 2

We assessed whether bees shifted their *relative preference* from the binary to trinary test phases along each dimension separately. We again ran binomial GLMMs (flower H = 0; flower M = 1), including ‘reward dimension’ (concentration or reward rate), ‘treatment’ (binary versus trinary) and ‘test type’ (pre or post) as fixed factors, including all two-way interactions and the three-way interaction. We included ‘bee’ as a random intercept but could not include ‘colony’ due to a singularity issue.

We assessed if bees shifted their *absolute preference* for flowers M and H by running two binomial GLMMs with choices for the target flower type (M or H) coded as 1 and all other choices coded as 0, using the same explanatory variables as for the relative preference analysis.

To determine if the two trinary treatments varied in experience with decoy flowers, we ran a LMM with number of visits to the decoy as the response variable, trinary treatment as the main effect and colony included as a random effect. We also asked whether bees differed in their experience with the decoy during the fourth trial, and if so, whether this explained preference shifts between the pre- and post-tests. We used GLMMs for each of the two trinary groups, including the relative preference for flower M as the response variable and the number of visits to the decoy in the fourth trial (continuous variable), test type (pre or post) and their interaction as explanatory variables, with bee ID included as a random factor in the model. Colony was not included due to singularity issues.

3. Results

(a) Experiment 1: context-dependent preferences along two reward dimensions

(i) Relative preference

Using the binary treatment and pre-test type as the baseline to compare the experimental treatments to, we found that the concentration trinary group did not differ in terms of bees' shifts in relative preferences between the two test types (concentration trinary × post test type: $z = 1.634$, $p = 0.102$; figure 4). However, bees in the rate trinary treatment increased their relative preference for flower R between the pre- and post-tests relative to the binary treatment (rate trinary × post test type: $z = 2.036$, $p = 0.042$; figure 4). Treatments alone did not differ (binary vs concentration trinary: $z = -1.339$, $p = 0.181$; binary vs rate trinary: $z = 0.767$, $p = 0.443$), nor did test type ($z = 0.489$, $p = 0.625$). Post hoc pairwise comparisons of test type within each treatment showed that bees in the binary treatment did not change preferences between the pre-test and the post-test ($p = 0.625$), indicating that preferences (which were slightly higher for flower R) were established early on and did not change with additional foraging experience.

(ii) Absolute preference

Comparing the two trinary treatments with the binary, we found a slight decrease in absolute preference for flower R between test types in the rate trinary group (rate trinary × post test type: $z = -1.738$, $p = 0.082$), but not the concentration trinary group (concentration trinary × post test type: $z = -0.227$, $p = 0.82$; electronic supplementary material, figure S2). There were no differences in absolute preference for flower type R based on treatment alone (concentration trinary: $z = -1.337$, $p = 0.181$, rate trinary: $z = 0.717$, $p = 0.474$; electronic supplementary material, figure S2), nor test type ($z = 0.49$, $p = 0.624$). Post hoc pairwise comparisons of test type within each treatment revealed that the absolute preference for flower R did not change between test type in the binary ($p = 0.625$) and concentration trinary ($p = 0.837$) groups but decreased slightly in the rate trinary group ($p = 0.044$). Absolute preferences for flower C decreased between the two tests in both the rate trinary treatment (rate trinary × post test type: $z = -4.041$, $p<0.001$; electronic supplementary material, figure S2) and concentration trinary treatment (concentration trinary × post test type: $z = 3.048$, $p = 0.002$; electronic supplementary material, figure S2) compared with the binary treatment. Pairwise comparisons within treatment showed that absolute preference for flower C decreased significantly in both rate trinary ($p < 0.001$) and concentration trinary ($p < 0.001$) groups, but not within the binary group ($p = 0.631$).

(iii) Visits to the decoy and effect of this on preference

Bees visited the decoy in the rate trinary treatment (mean ± s.d. = 24 ± 11.49) slightly more than in the concentration trinary treatment (mean ± s.d. = 19 ± 5.62) in the fourth trial ($t = 1.887$, d.f. = 32, $p = 0.068$; electronic supplementary material, figure S2). Bees in the concentration trinary treatment that visited the decoy more frequently in the fourth trial showed stronger preference shifts towards flower C (decoy visits × test type: $z = -4.12$, $p < 0.001$; electronic supplementary material, figure S3a), as predicted by the asymmetrically dominated decoy effect (table 1). There was no effect of experience with the decoy on preference shifts for the rate trinary treatment (decoy visits × test type: $z = 0.524$, $p = 0.60$; electronic supplementary material, figure S3b).

(b) Experiment 2: context-dependent preferences along single reward dimensions

(i) Relative preference

We addressed the effects of a lower quality decoy on the relative preference for medium- and high-quality flowers varying in concentration. Adding the low-concentration decoy increased the relative preference for the medium-concentration flower in the trinary treatment relative to bees in the binary treatment (treatment × test type: $z = 2.399$, $p = 0.017$, figure 5*a*). Specifically, a post hoc test showed the relative preference for the medium-concentration flower decreased between the pre- and post-test types in the binary group ($p < 0.001$), but not in the trinary group ($p = 0.746$). There was also a significant colour effect, with bees preferring blue flowers across both treatments and test types (flower colour: $z = -5.212$, $p < 0.001$). An increased preference for the high-concentration flower in the binary group is as expected, as bees are likely still learning in the pre-test (trials 2 and 3).

Bees in both treatments increased their relative preference for the high-rate flower, indicating that bees increasingly discriminated against the medium-rate flower with experience. While there was no significant interaction between treatment and test type (treatment × test type: $z = -1.800$, $p = 0.07$, figure 5*b*), post hoc tests revealed that this effect was slightly stronger for the trinary group ($p < 0.001$) than the binary group ($p = 0.063$)—in the opposite direction to what was originally predicted. Again, we found that bees preferred blue over yellow flowers (flower colour: $z = 7.024$, $p < 0.001$). Additionally, there was a significant interaction between flower colour and test type (flower colour × test type: $z = -3.034$, $p = 0.002$); post hoc comparisons revealed that preferences only changed across test types for yellow flower visits ($p < 0.001$), while bees' visits to the more preferred blue, did not change across test types ($p = 0.399$).

(ii) Absolute preference

As expected, the absolute preference for flower M along the concentration dimension decreased between choice tests (test type: $z = -3.721$, $p < 0.001$), but this effect did not differ between treatments (treatment × test type: $z = -0.238$, $p = 0.812$; electronic

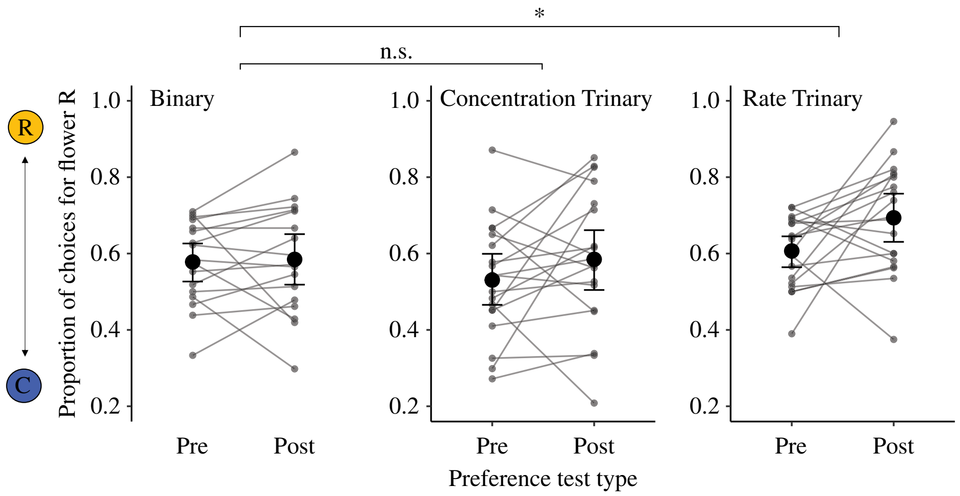

Figure 4. Experiment 1. Shifts in relative preference between R and C across the treatments and test types. Relative preferences for flower R are shown for binary (left), concentration trinary (middle) and rate trinary (right) treatments. For each treatment, preferences are shown for both before (pre-test) and after (post-test) bees experience the decoy flower in the trinary treatments. Higher values indicate a preference for flower R and lower values indicate a preference for flower C. The asterisk indicates a significant interaction between treatment and test type, at $p < 0.05$.

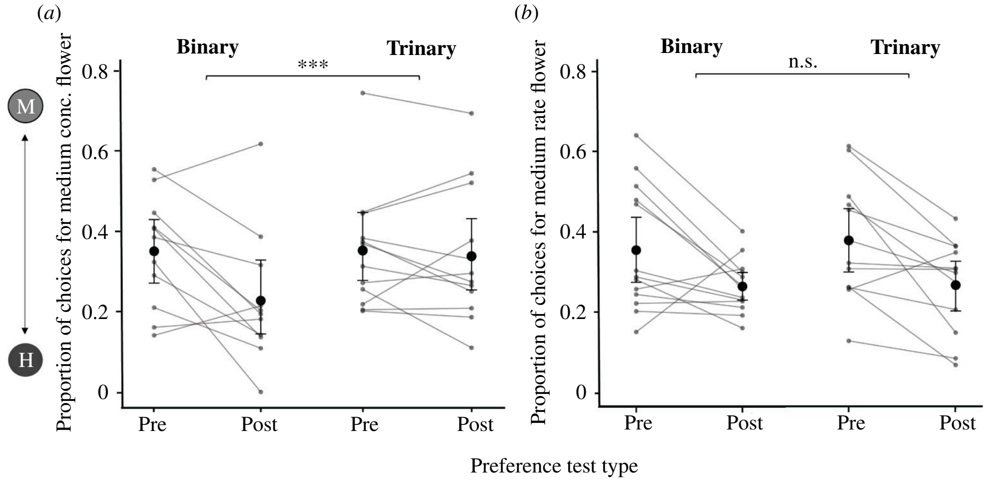

Figure 5. Experiment 2: relative preferences for the medium-quality (M) versus high-quality (H) flowers by treatment for the (*a*) concentration dimension and (*b*) reward rate dimension in the pre- and post-preference tests. The asterisk indicates a significant interaction between treatment and test type, at $p < 0.05$.

supplementary material, figure S4). Absolute preference for flower M was higher for blue than yellow flowers across both treatments and test types (flower colour: $z = -5.828$, $p < 0.001$). Absolute preference for flower H also decreased between choice tests, but this effect was stronger in the trinary than binary treatment (treatment × test type: $z = -3.869$, $p < 0.001$; electronic supplementary material, figure S4). This may be explained by both stable preferences for flower M and a surprisingly high number of choices for flower L, which may have pulled choices away from flower H. We also found higher absolute preferences for flower H when it was blue (flower colour: $z = 3.766$, $p < 0.001$), as well as a three-way interaction between flower colour, treatment and test type ($z = -2.009$, $p = 0.045$; electronic supplementary material, figure S5). Within the binary treatment, absolute preference for flower H increased more between pre- and post-tests for bees trained that blue flowers were more rewarding ($p < 0.001$) than yellow flowers ($p = 0.064$). In the trinary group, absolute preference for flower H increased more between pre- and post-tests for bees trained that yellow flowers were more rewarding ($p < 0.001$) than blue flowers ($p = 0.036$).

Absolute preference for flower M along the reward rate dimension decreased between pre- and post-tests, although this varied by treatment (treatment × test type: $z = 0.176$, $p = 0.004$; electronic supplementary material, figure S6). Absolute preference decreased more between test types in the trinary treatment ($p < 0.001$) than in the binary treatment ($p = 0.064$). There was also an interaction between flower colour and test type (flower colour × test type: $z = -2.683$, $p = 0.007$). Across both treatments, absolute preference for flower M decreased more for bees trained that yellow flowers were more rewarding ($p < 0.001$) than blue flowers ($p = 0.066$). There were no effects of treatment or test type alone on absolute preference for flower H (treatment: $z = -0.064$, $p = 0.945$; test type: $z = 0.006$, $p = 0.995$); however, we did find an effect of flower colour, with bees showing higher absolute preferences for blue flowers (flower colour: $z = -4.727$, $p < 0.001$). There was also a three-way interaction between flower colour, treatment and test type (flower colour × treatment × test type: $z = 2.185$; $p = 0.029$, electronic supplementary material, figure S7). Within the binary treatment, absolute preference for flower H increased more between pre- and post-tests for bees trained that yellow flowers were more rewarding ($p < 0.008$) than blue flowers ($p = 0.995$). In the trinary group, absolute preference for flower H increased between pre- and post-tests for bees trained to both flower colours, but this effect was stronger for bees trained that yellow flowers were more rewarding ($p < 0.001$) than those trained to blue flowers ($p = 0.002$).

(iii) Visits to the decoy and effect of this on preference

Bees in the two trinary treatments did not differ in their number of visits to the decoy option in the fourth trial (concentration treatment mean ± s.d. = 32 ± 14.25; reward rate treatment mean ± s.d. = 35 ± 11.81; $t = -0.452$, d.f. = 22, $p = 0.655$). There was also no effect of the number of visits to the decoy option on relative preference shifts for either the concentration dimension (decoy visits × test type: $z = 1.229$, $p = 0.219$; electronic supplementary material, figure S8a) or rate dimension (decoy visits × test type: $z = 0.403$, $p = 0.687$; electronic supplementary material, figure S8b).

4. Discussion

While decoy effects and other forms of irrational decisions appear common across a wide array of taxa, they are not ubiquitous, and it is unclear when animals are expected to make context-dependent decisions. Here we investigated how bumblebees make decisions between flowers that vary in their nectar concentration and reward rate. We found that the introduction of a rate decoy led to context-dependent preferences, but the introduction of a concentration decoy did not. In a second experiment, we found evidence that bees may only use relative evaluation for concentration, and not reward rate, through testing each of these variables separately. Thus, preference shifts observed here in one direction may be explained by relative evaluation along only one of these two reward dimensions.

In our first experiment, bees shifted preferences towards a high-rate, medium-concentration flower when presented with a decoy that was lower in rate and concentration. However, bees did not shift preferences towards a high-concentration, medium-rate flower when presented with a decoy lower along these two dimensions. Preferences in the concentration trinary group actually slightly increased for the high-rate flower, in the opposite direction than predicted by the decoy effect. Even with this slight increase, however, this treatment group did not differ from the binary treatment. Interestingly, in the concentration trinary treatment, we found bees that visited the decoy flowers more showed stronger preference shifts in the predicted direction (towards flower C). This indicates that, if individuals had more experience with the decoy option, more of them may have shifted preferences in the predicted direction. In our second experiment, we presented bees with binary and trinary choices between flowers that varied along a single reward dimension. When flowers varied in concentration, the addition of a low-concentration option caused bees to choose a medium-concentration flower more frequently than before. In contrast, when flowers varied in reward rate, the addition of a low-rate option did not affect bees' preferences for the high-rate option. Results from both experiments indicate that while bumblebees readily attend to both reward axes, both separately and together, they may only use comparative evaluation mechanisms for evaluating concentration, but not reward rate. We also found a slight colour preference for blue over yellow flowers in Experiment 2. Because flower C was always blue in Experiment 1, and bees shifted preferences away from this flower type in the rate trinary condition, we may have observed even stronger preference shifts in the absence of this colour preference. Additionally, bees may have had a slight preference for the white colour used for decoys, as bees in both trinary conditions visited decoy flowers.

What might explain the difference between bees' assessment of these two reward axes? Animals are expected to make efficient decisions [20,21], which may mean using the most easily perceived shared dimension to make comparisons between options [50]. Foraging bees can detect the sugar concentration of nectar within milliseconds of sampling it [51], whereas reward rate requires sequential sampling of multiple flowers [52]. This explanation is supported by work in other systems: *Temnothorax* ants make irrational choices when choosing between nest sites that vary in cavity size and light levels, both of which can be visually assessed immediately [53]. Similarly, hummingbirds (*Selasphorus rufus*) use comparative evaluation for concentration and volume dimensions, but not corolla length, which may take longer to assess [27,28]. Finally, starlings (*Sturnus vulgaris*) do not show context-dependent decisions when assessing the probability of a food reward [54], which requires repeated sampling to assess. Even in humans, individuals are typically given complete information about different options when decisions are being made (e.g. [10,55]), potentially facilitating comparative evaluation strategies.

While decoy effects and other forms of irrational behaviour have been demonstrated in many species and contexts (reviewed in [25]), the focus has largely been on behavioural outcomes, with less consideration given to underlying psychological mechanisms. We believe that our results can be explained in terms of incentive contrast effects, where the value of an option shifts relative to recently encountered options. For instance, an individual may overvalue a medium-quality reward after recently encountering a lower-quality reward (positive incentive contrast) and undervalue that same medium-quality option directly following a higher quality one (negative incentive contrast). Bees show robust contrast effects in relation to sucrose concentration [15,42,56–59]. This can be a purely sensory response [56], or be mediated through associated floral stimuli [42]. While contrast effects are nearly always addressed with two options, they are just as likely to be at play with more than two. For example, in Experiment 2, bees first encountered medium- versus high-quality flowers, where the medium-quality option would seem relatively worse. However, once a third, low-quality option was added, the medium option would be perceived as relatively better, and thus be more likely to be chosen. This is indeed what we found for sucrose concentration, in line with previous work on contrast effects [15,56,58]. However, we did not find this response for reward rate, and it may be that contrast effects are less likely when options are difficult to quickly compare. Even though flowers in Experiment 1 varied in two dimensions, our findings from Experiment 2 demonstrate that the addition of a 20% concentration flower increases the preference for a 30% flower relative to a 50% flower, and thus, this effect may also have been at play in Experiment 1. Specifically, if the low-concentration D_R was driving incentive contrast (i.e. increasing a preference for the medium-concentration 'R' option) to a greater degree than the low-rate D_C was driving a preference towards the 'C' option, this could explain the results we found.

Another possible reason for the asymmetric effects we found in Experiment 1 is that variation in the concentration dimension is perceived as greater than the variation in reward rate dimension. If so, differences in concentration may overshadow differences in reward rate in Experiment 1, when both were simultaneously manipulated. This has been proposed to account for irrational behaviour in hummingbirds choosing between flowers that vary in concentration and volume [28]. We consider this unlikely in this case, however, as bees' relative preferences in the two binary conditions of Experiment 2 were similar, indicating that variation along each reward axis was valued similarly in both experiments.

One common explanation for decoy effects and other irrational behaviours in animals is that a decision-maker's motivational or physiological state changes across the decision-making period [60,61]. While properties of options can be communicated to humans, non-human animals must first be trained to the contingencies of different options, and this repeated exposure can affect an animal's state in ways that may influence later decisions [61]. Social bees like bumblebees are particularly useful in avoiding this limitation, since foragers collect food for their colony rather than themselves, regurgitating nectar between foraging bouts and returning to forage fully motivated. In this system, foraging motivation and related decision-making may be more affected by the state of the colony rather than the individual [62]. However, given the short timescale in which bees were tested in the current experiment (typically less than 1 h per bee), it is unlikely that the colony state changed during the testing period. More generally, future studies could explore whether colony-level preferences are sensitive to the choice context, and if so, whether these biases vary according to the state of the colony.

Previous work with honeybees found evidence for context-dependent decisions across multiple dimensions: bees were subject to decoy effects when evaluating flower types varying in depth and volume [32] and concentration and temperature [31]. Differences between those studies and the present one may be due to species differences, or differences in attributes being evaluated. Variation in decision-making strategies have previously been reported in closely related species, such as Neotropical bats [25,26]. In that case, differences in ecology or diet best explain the use of heuristics [25,26]. Although honeybees and bumblebees are close relatives [63] and both generalist nectar foragers, there may be other, more subtle differences in diet and social structure that could lead to differences in decision-making strategies [64]. First, bumblebee colonies are much smaller than those of honeybees, meaning that the consequences of individual foraging decisions may have a greater impact on colony-level fitness. As such, we might expect individual bumblebees to make more 'optimal' foraging decisions [64]. This appears to be the case in the context of other foraging decisions: honeybees persist longer at feeders when the quality is reduced, whereas bumblebees shift sooner to a different feeder [65]. Second, bumblebees lack the sophisticated 'dance' signalling system found in honeybees [66], and as such may rely more on personally acquired information [64,65]. Future studies could compare decision-making strategies between these two species in relation to specific nectar attributes.

One limitation of our study is that the costs of poor decisions may not accurately reflect decision errors for bees foraging on wildflowers spaced further apart and experienced over longer periods of time. In more naturalistic scenarios, comparative evaluation may be more pronounced to allow bees to efficiently exploit nectar resources. On the other hand, with an increase in time between sampling flowers, it may be more difficult for bees to make direct comparisons. Future studies examining context-dependent decisions at different spatial and temporal scales would help shed light on how decision costs influence decision strategies.

Our results imply that in natural systems, co-flowering species may facilitate or compete with one another in attracting pollinators in previously unconsidered ways. For instance, if bumblebees are more sensitive to relative differences in reward attributes that are quickly assessed, this may create more direct competition between plants along those reward axes. Facilitation typically occurs between flowers with similar floral traits [67], but dissimilar flowers with relatively inferior rewards also appear to facilitate visitation to focal species (e.g. [68–70]), perhaps by providing a direct comparison while still receiving visits. If co-flowering species with lower quality rewards receive more visits than they would on their own, this may be advantageous for both flower types.

Understanding the underlying mechanisms and strategies employed by animals when making decisions is essential for gaining insights into their behaviour, cognitive abilities and evolutionary dynamics. In the wild, decision-making is more complex, since bees also process additional aspects of nectar rewards (e.g. secondary chemicals), multiple types of floral rewards (e.g. nectar and pollen) [33], and complex floral signals [13]. Going forward, capturing more of this complexity experimentally will help us better understand the cognitive mechanisms that lead bees and other pollinators to choose certain flowers over others.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Datasets and analyses are available on Dryad [49].

Supplementary material is available online [71].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. C.T.H.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization, writing—original draft, writing—review and editing; J.E.DeV.: investigation, methodology, writing—original draft, writing—review and editing; F.M.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. Funding for this work was provided by NSF award nos. IOS-2028613 and IOS-2445480.

Acknowledgements. We thank the Muth Lab, the University of Tennessee Animal Behavior Group and three anonymous reviewers for feedback on the manuscript.

References

1. NeumannJ, Morgenstern O. 1944 *Theory of games and economic behavior*. Princeton, NJ: Princeton University Press.
2. Stephens D, Krebs J. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.
3. Charnov EL. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136. (doi:10.1016/0040-5809(76)90040-x)
4. MacArthur RH, Pianka ER. 1966 On optimal use of a patchy environment. *Am. Nat.* **100**, 603–609. (doi:10.1086/282454)
5. Emlen JM. 1966 The role of time and energy in food preference. *Am. Nat.* **100**, 611–617. (doi:10.1086/282455)
6. Orr HA. 2007 Absolute fitness, relative fitness, and utility. *Evolution* **61**, 2997–3000. (doi:10.1111/j.1558-5646.2007.00237.x)
7. McNamara JM, Houston AI. 1986 The common currency for behavioral decisions. *Am. Nat.* **127**, 358–378. (doi:10.1086/284489)
8. Tversky A, Kahneman D. 1986 Rational choice and the framing of decisions. *J. Bus.* **59**, S251. (doi:10.1086/296365)
9. Tversky A, Simonson I. 1993 Context-dependent preferences. *Manage. Sci.* **39**, 1179–1189. (doi:10.1287/mnsc.39.10.1179)
10. Huber J, Payne JW, Puto C. 1982 Adding asymmetrically dominated alternatives: violations of regularity and the similarity hypothesis. *J. Consum. Res.* **9**, 90. (doi:10.1086/208899)
11. Bateson M, Healy SD, Hurly TA. 2002 Irrational choices in hummingbird foraging behaviour. *Anim. Behav.* **63**, 587–596. (doi:10.1006/anbe.2001.1925)
12. Flaherty CF. 1982 Incentive contrast: a review of behavioral changes following shifts in reward. *Anim. Learn. Behav.* **10**, 409–440. (doi:10.3758/BF03212282)
13. Latty T, Trueblood JS. 2020 How do insects choose flowers? A review of multi-attribute flower choice and decoy effects in flower-visiting insects. *J. Anim. Ecol.* **89**, 2750–2762. (doi:10.1111/1365-2656.13347)
14. Spektor MS, Bhatia S, Gluth S. 2021 The elusiveness of context effects in decision making. *Trends Cogn. Sci.* **25**, 843–854. (doi:10.1016/j.tics.2021.07.011)
15. Bitterman ME. 1976 Incentive contrast in honey bees. *Science* **192**, 380–382. (doi:10.1126/science.1257773)
16. Wendt S, Strunk KS, Heinze J, Roider A, Czaczkes TJ. 2019 Positive and negative incentive contrasts lead to relative value perception in ants. *eLife* **8**, e45450. (doi:10.7554/eLife.45450)
17. Pellegrini S, López Seal MF, Papini MR. 2008 Scaling relative incentive value: different adjustments to incentive downshift in pigeons and rats. *Behav. Process.* **79**, 182–188. (doi:10.1016/j.beproc.2008.07.008)
18. Shafir S. 1994 Intransitivity of preferences in honey bees: support for 'comparative' evaluation of foraging options. *Anim. Behav.* **48**, 55–67. (doi:10.1006/anbe.1994.1211)
19. Waite T. 2001 Intransitive preferences in hoarding gray jays. *Behav. Ecol. Sociobiol.* **50**, 116–121. (doi:10.1007/s002650100346)
20. Todd PM, Gigerenzer G. 2007 Environments that make us smart: ecological rationality. *Curr. Dir. Psychol. Sci.* **16**, 167–171. (doi:10.1111/j.1467-8721.2007.00497.x)
21. Fawcett TW, Fallenstein B, Higginson AD, Houston AI, Mallpress DEW, Trimmer PC, McNamara JM. 2014 The evolution of decision rules in complex environments. *Trends Cogn. Sci.***18**, 153–161. (doi:10.1016/j.tics.2013.12.012)
22. Shanteau J, Thomas RP. 2000 Fast and frugal heuristics: what about unfriendly environments? *Behav. Brain Sci.* **23**, 762–763. (doi:10.1017/S0140525X00463442)
23. Monk RL, Qureshi AW, Leatherbarrow T, Hughes A. 2016 The decoy effect within alcohol purchasing decisions. *Subst. Use Misuse* **51**, 1353–1362. (doi:10.3109/10826084.2016.1168449)
24. Xu L, Yu M, Chen X. 2021 Decoy effect on consumers' purchase behaviors in relation to meat products: comparison of pork and chicken. *Front. Psychol.* **12**, 679256. (doi:10.3389/fpsyg.2021.679256)
25. Hemingway CT, Ryan MJ, Page RA. 2017 Rationality in decision-making in the fringe-lipped bat, *Trachops cirrhosus*. *Behav. Ecol. Sociobiol.* **71**. (doi:10.1007/s00265-017-2321-5)
26. Hemingway CT, Aversa III JC, Ryan MJ, Page RA. 2021 Context-dependent preferences in wild fruit bats. *Anim. Behav.* **179**, 65–72. (doi:10.1016/j.anbehav.2021.06.016)
27. Morgan KV, Hurly TA, Bateson M, Asher L, Healy SD. 2012 Context-dependent decisions among options varying in a single dimension. *Behav. Process.* **89**, 115–120. (doi:10.1016/j.beproc.2011.08.017)
28. Bateson M, Healy SD, Hurly TA. 2003 Context-dependent foraging decisions in rufous hummingbirds. *Proc. R. Soc. Lond. B***270**, 1271–1276. (doi:10.1098/rspb.2003.2365)
29. Heinrich B. 1979 *Bumblebee economics*, 6th edn. Cambridge, MA: Harvard University Press.
30. Real LA. 1996 Paradox, performance, and the architecture of decision-making in animals. *Am. Zool.* **36**, 518–529. (doi:10.1093/icb/36.4.518)
31. Tan K, Dong S, Liu X, Chen W, Wang Y, Oldroyd BP, Latty T. 2015 Phantom alternatives influence food preferences in the eastern honeybee *Apis cerana*. *J. Anim. Ecol.* **84**, 509–517. (doi:10.1111/1365-2656.12288)
32. Shafir S, Waite T, Smith B. 2002 Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.***51**, 180–187. (doi:10.1007/s00265-001-0420-8)
33. Hemingway CT, Leonard AS, MacNeill FT, Pimplikar S, Muth F. 2024 Pollinator cognition and the function of complex rewards. *Trends Ecol. Evol.* S0169-5347(24)00146-0. (doi:10.1016/j.tree.2024.06.008)
34. Nicolson SW. 2022 Sweet solutions: nectar chemistry and quality. *Phil. Trans. R. Soc. B* **377**, 20210163. (doi:10.1098/rstb.2021.0163)
35. Cnaani J, Thomson JD, Papaj DR. 2006 Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. *Ethology* **112**, 278–285. (doi:10.1111/j.1439-0310.2006.01174.x)
36. Thomson JD, Ogilvie JE, Makino TT, Arisz A, Raju S, Rojas-Luengas V, Tan M. 2012 Estimating pollination success with novel artificial flowers: effects of nectar concentration. *J. Pollinat. Ecol.* **9**, 108–114. (doi:10.26786/1920-7603(2012)14)
37. Thomson JD. 1986 Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *J. Ecol.* **74**, 329. (doi:10.2307/2260258)
38. Pleasants JM, Zimmerman M. 1983 The distribution of standing crop of nectar: what does it really tell us? *Oecologia* **57**, 412–414. (doi:10.1007/BF00377188)
39. Forster CY, Middleton EJT, Gloag R, Hochuli DF, White TE, Latty T. 2023 Impact of empty flowers on foraging choice and movement within floral patches by the honey bee, *Apis mellifera*. *Insectes Soc.* **70**, 413–422. (doi:10.1007/s00040-023-00934-3)
40. Real LA. 1981 Uncertainty and pollinator–plant interactions: the foraging behavior of bees and wasps on artificial flowers. *Ecology* **62**, 20–26. (doi:10.2307/1936663)
41. Cartar RV. 2004 Resource tracking by bumble bees: responses to plant-level differences in quality. *Ecology* **85**, 2764–2771. (doi:10.1890/03-0484)
42. Hemingway CT, Muth F. 2022 Label-based expectations affect incentive contrast effects in bumblebees. *Biol. Lett.* **18**, 20210549. (doi:10.1098/rsbl.2021.0549)
43. Dunlap AS, Papaj DR, Dornhaus A. 2017 Sampling and tracking a changing environment: persistence and reward in the foraging decisions of bumblebees. *Interface Focus* **7**, 20160149. (doi:10.1098/rsfs.2016.0149)
44. Luce RD, Suppes P. 1965 Preference, utility, and subjective probability. In *Handbook of mathematical psychology*, pp. 249–410. New York, NY: John Wiley.
45. R Core Team. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org/.
46. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss067.i01)

47. Fox J, Weisberg S. 2011 *An R companian to applied regression, 2nd edition*. Thousand Oaks, CA: SAGE Publications Inc.
48. Length R. 2022 Emmeans: estimated marginal means, aka least-squares means
49. Hemingway CT, DeVore JE, Muth F. 2024 Datasets and R code from: 'economic foraging in a floral marketplace: asymmetrically dominated decoy effects in bumblebees. Dryad Digital Repository. (doi:10.5061/dryad.08kprr5bb)
50. Bateson M, Healy SD. 2005 Comparative evaluation and its implications for mate choice. *Trends Ecol. Evol.* **20**, 659–664. (doi:10.1016/j.tree.2005.08.013)
51. de Brito Sanchez MG. 2011 Taste perception in honey bees. *Chem. Senses* **36**, 675–692. (doi:10.1093/chemse/bjr040)
52. Shafir S, Bechar A, Weber EU. 2003 Cognition-mediated coevolution – context-dependent evaluations and sensitivity of pollinators to variability in nectar rewards. *Plant Syst. Evol.* **238**, 195–209. (doi:10.1007/s00606-003-0280-y)
53. Sasaki T, Pratt SC. 2011 Emergence of group rationality from irrational individuals. *Behav. Ecol.* **22**, 276–281. (doi:10.1093/beheco/arq198)
54. Monteiro T, Vasconcelos M, Kacelnik A. 2013 Starlings uphold principles of economic rationality for delay and probability of reward. *Proc. R. Soc. B Biol. Sci.* **280**, 20122386. (doi:10.1098/rspb.2012.2386)
55. Choplin JM, Hummel JE. 2005 Comparison-induced decoy effects. *Mem. Cognit.* **33**, 332–343. (doi:10.3758/BF03195321)
56. Wiegmann DD, Smith BH. 2009 Incentive relativity and the specificity of reward expectations in honey bees. *Int. J. Comp. Psychol.* **22**, 141–152. (doi:10.46867/IJCP.2009.22.03.03)
57. Wiegmann D, Wiegmann D, Waldron F. 2003 Effects of a reward downshift on the consummatory behavior and flower choices of bumblebee foragers. *Physiol. Behav.* **79**, 561–566. (doi:10.1016/S0031-9384(03)00122-7)
58. Waldron FA, Wiegmann DD, Wiegmann DA. 2005 Negative incentive contrast induces economic choice behavior by bumble bees. *Int. J. Comp. Psychol.* **18**, 358–371. (doi:10.46867/IJCP.2005.18.04.02)
59. Couvillon PA, Bitterman ME. 1984 The overlearning-extinction effect and successive negative contrast in honeybees (*Apis mellifera*). *J. Comp. Psychol.* **98**, 100–109.
60. Pompilio L, Kacelnik A. 2005 State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Anim. Behav.* **70**, 571–578. (doi:10.1016/j.anbehav.2004.12.009)
61. Schuck-Paim C, Pompilio L, Kacelnik A. 2004 State-dependent decisions cause apparent violations of rationality in animal choice. *PLoS Biol.* **2**, e402. (doi:10.1371/journal.pbio.0020402)
62. Hendriksma HP, Toth AL, Shafir S. 2019 Individual and colony level foraging decisions of bumble bees and honey bees in relation to balancing of nutrient needs. *Front. Ecol. Evol.* **7**, 177. (doi:10.3389/fevo.2019.00177)
63. Michener C. 2000 *The bees of the world*. Baltimore, MD: Johns Hopkins University Press.
64. Sherry DF, Strang CG. 2015 Contrasting styles in cognition and behaviour in bumblebees and honeybees. *Behav. Processes* **117**, 59–69. (doi:10.1016/j.beproc.2014.09.005)
65. Townsend-Mehler JM, Dyer FC, Maida K. 2011 Deciding when to explore and when to persist: a comparison of honeybees and bumblebees in their response to downshifts in reward. *Behav. Ecol. Sociobiol.* **65**, 305–312. (doi:10.1007/s00265-010-1047-4)
66. Dornhaus A, Chittka L. 2001 Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. *Behav. Ecol. Sociobiol.* **50**, 570–576. (doi:10.1007/s002650100395)
67. Rathcke B. 1983 Competition and facilitation among plants for polliantion. In *Pollination biology*, pp. 305–329. London: Academic Press. (doi:10.1016/B978-0-12-583980-8.50019-3)
68. Ghazoul J. 2006 Floral diversity and the facilitation of pollination. *J. Ecol.* **94**, 295–304. (doi:10.1111/j.1365-2745.2006.01098.x)
69. Liao K, Gituru RW, Guo YH, Wang QF. 2011 The presence of co-flowering species facilitates reproductive success of *Pedicularis monbeigiana* (Orobanchaceae) through variation in bumble-bee foraging behaviour. *Ann. Bot.* **108**, 877–884. (doi:10.1093/aob/mcr216)
70. Moeller DA. 2004 Facilitative interactions among plants via shared pollinators. *Ecology* **85**, 3289–3301. (doi:10.1890/03-0810)
71. Hemingway CT, DeVore J, Muth F. 2024 Data from: economic foraging in a floral marketplace: asymmetrically dominated decoy effects in bumblebees. Figshare. (doi:10.6084/m9.figshare.c.7441750)