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Review

Pollinator cognition and the function of complex rewards

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The cognitive ecology of pollination is most often studied using simple rewards, yet flowers often contain multiple types of chemically complex rewards, each varying along multiple dimensions of quality. In this review we highlight ways in which reward complexity can impact pollinator cognition, demonstrating the need to consider ecologically realistic rewards to fully understand plant–pollinator interactions. We show that pollinators' reward preferences can be modulated by reward chemistry and the collection of multiple reward types. We also discuss how reward complexity can mediate pollinator learning through a variety of mechanisms, both with and without reward preference being altered. Finally, we show how an understanding of decision-making strategies is necessary to predict how pollinators' evaluation of reward options depends on the other options available.

Highlights

Over a century of research on pollinator cognition has shown that pollinators such as bees perceive and learn a multitude of floral stimuli and are capable of sophisticated decision-making using a variety of cognitive abilities.

Research on pollinator cognition usually focuses on a single reward aspect in isolation, which does not reflect the complexity of reward types, chemistries, and attributes many pollinators encounter while foraging.

Reward complexity can impact pollinators' perception, learning, and decision-making in interesting and sometimes unexpected ways.

A cognitive perspective can shed new insight into the functions of floral reward complexity and bridge the fields of animal behavior and plant ecology.

Pollinator cognition and complex rewards

Plants present pollinators with a multi-sensory billboard of information [1]. Floral signals and cues can be incredibly complex and can function to inform and sometimes manipulate pollinators [2,3]. Pollinators, however, ultimately use floral signals to find rewards – although these can be intertwined (Box 1). How pollinator **cognition** (see Glossary) shapes and is shaped by complex floral signals has been well studied over decades of research [2,4]. More recently, interest has grown in understanding how complex rewards alter cognitive performance. In this review we discuss how complex rewards can impact pollinator cognition through effects upon (i) perception and assessment, (ii) learning and memory, and (iii) comparative evaluation, while acknowledging that there is overlap and feedback across these processes (Figure 1). We focus on social bees – honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.), as much of the research on this topic involves these generalist taxa [4] – while including examples from other pollinators where relevant.

What is a floral reward?

Within the field of cognition, a reward is broadly understood in terms of reinforcing **associative learning**, driving 'wanting' or desire and, in some cases, causing pleasure [5]. When forming associations, animals learn that a particular **conditioned stimulus** (e.g., floral color), or a behavior (e.g., prying open petals of a particular flower), will lead to a reward (**unconditioned stimulus**). By contrast, within the field of pollination ecology, floral rewards are defined by their benefit to pollinators [6]. These two definitions can conflict: for example, plants can deceive pollinators, advertising rewards where there are none. Some orchids do this by mimicking female insects, which fools males into pollinating flowers through mating attempts [7]. These mating attempts may be rewarding to males from the cognitive perspective (if a male does not realize that he has been 'duped'), yet these species are rewardless from the ecological perspective, since the pollinator does not benefit, and may instead incur a cost from visiting this flower. In this review we discuss floral rewards using the definition from pollination ecology, while also expecting that

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floral rewards fit our understanding from the cognitive perspective, even where this has not been explicitly tested.

What is reward complexity?

Many cognitive abilities allow a pollinator to perceive and assess rewards, learn about where to find them, and choose between flowers that differ in their rewards, and all of these can be affected by reward complexity (Figure 1). Herein we focus on three types of complexity that can affect pollinator cognition – chemical complexity, multiple attributes of quality, and multiple types of reward – while acknowledging that there is no direct relationship between complexity and cognition. For example, a nectar may be more chemically complex, but have fewer effects on cognition than a chemically simpler nectar.

Many rewards, such as nectar and pollen, have tremendous chemical complexity. Nectar is a primary source of carbohydrates, and pollen of protein, but both contain a host of **secondary metabolites** (or specialized metabolites). Plants defend their tissues with thousands of chemicals to reduce herbivory, and many of these toxins may be present in nectar via ‘passive

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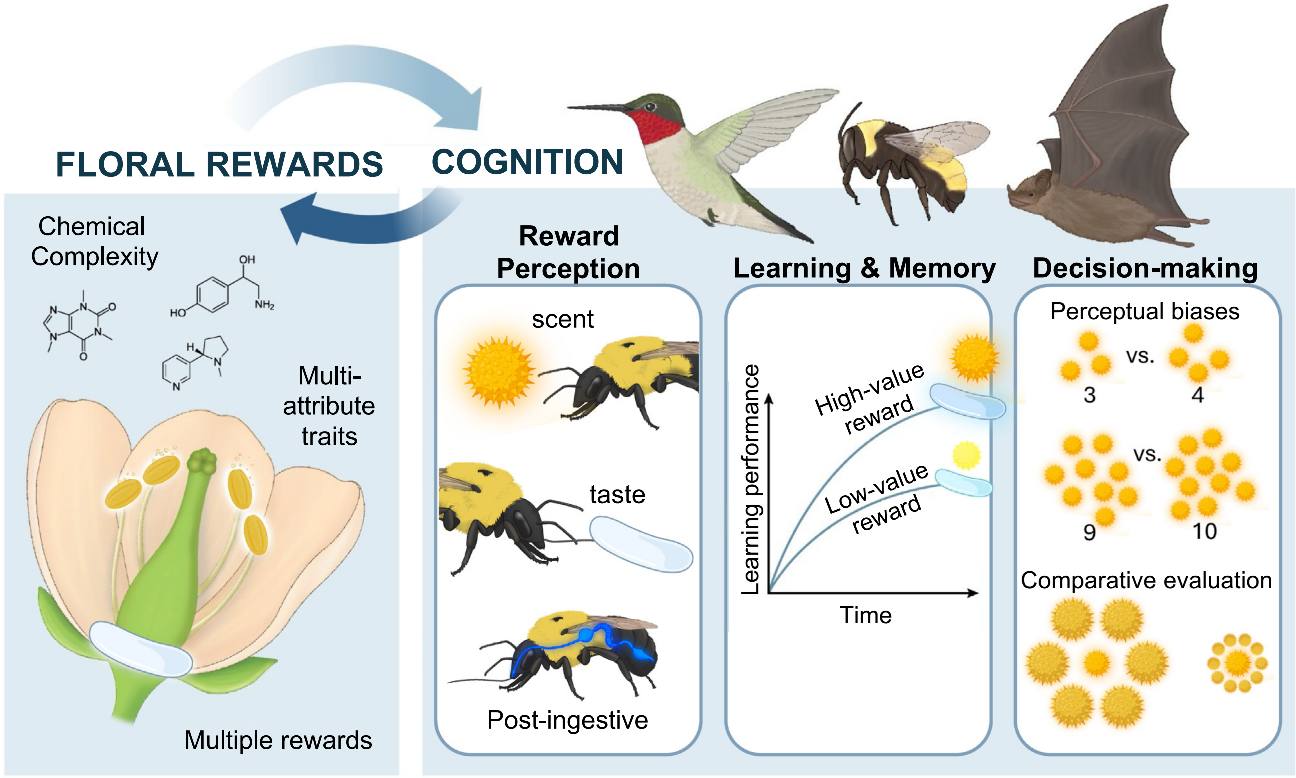

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Figure 1. Impacts of reward complexity on pollinator cognition. Overview of conceptual framework. Left box: floral rewards can be complex in a number of ways, including chemical complexity, having multiple attributes, and comprising multiple reward types. Right box: all of these types of complexity can affect pollinator cognition, including how pollinators perceive and form preferences for flowers, their learning and memory, and how they compare flowers with different rewards. Reward perception can be mediated by scent, taste, and post-ingestive effects. Learning and memory can be modulated by reward value or perception of value, direct effects of neuroactive chemicals, and interacting effects of multiple reward attributes and reward types. Finally, decision-making between floral types can be prone to perceptual biases such as Weber’s law where quantities are easier to discriminate at low values. In addition, rewards are often judged relative to other options available, which can be affected by multiple reward attributes and types of reward.

leaking' or due to other functions [8,9]. In addition, many animals 'rob' rewards without pollinating [10], and many rewards are physically and chemically defended against thieves. Thus, a reward to one floral visitor can be a toxic deterrent to others, and even intended recipients must tolerate defensive chemicals [11]. However, many 'toxic' metabolites have positive effects on floral visitors, including antimicrobial effects, medicinal benefits, and cognitive enhancement (for a review see [12]). Pollen, too, is incredibly complex chemically, containing even more chemical defenses than nectar [13]. This is because pollen is a contradictory reward from an evolutionary perspective: as the male gametophyte, animal-pollinated plants require pollinators to remove pollen (and indeed ≈20 000 plant species use pollen as the primary reward), yet removal without transfer to conspecifics comes at a fitness cost [14]. As such, plants have evolved complex pollen chemistry, amongst other strategies, to encourage pollen transfer while limiting its removal.

Floral rewards are also complex in that they can vary along multiple attributes of quality, most of which must be perceived and integrated by foraging bees when learning and evaluating different flowers [15]. Even just considering sucrose solution (the chemically simple nectar surrogate often used in behavioral experiments), there is variation in volume, concentration, variability, and reward rate. Because nectar production is costly, plants often cannot invest equally in all aspects of nectar quality, leading to differential investment in nectar attributes [16].

Plants also contain multiple types of rewards, and many pollinators collect more than one type [6]. Pollen is the oldest reward; the subsequent evolution of nectar presumably led to new selection on pollinator behavior and cognition, sending the coevolution of plants and pollinators in new directions [17]. While pollen and nectar are the primary nutritive rewards, flowers also offer heat, oils, resins, perfumes, and shelter [6], all of which are used by bees. These rewards have diverse evolutionary histories, involving distinct pollinator species that vary in their reward collection methods and uses. For example, oils are produced across hundreds of plant species, most of which offer this as their sole reward for bee pollinators, which use collected oil to provision larvae and for nest construction [18]. 'Perfumes' are created by male orchid bees collecting volatile compounds from flowers to court females [19]. Resin harvested by many bee species is used in nest construction for its structural attributes, chemical camouflage, and antimicrobial properties [20]. Little work has been done on pollinator cognition with non-nutritive floral rewards (but see [21–23]), and this area is ripe for future research. Because of this, we focus here on the two most ubiquitous and well-studied floral rewards: nectar and pollen, collected by numerous invertebrate and vertebrate pollinators.

Perception of floral rewards and its influence on pollinators' preferences

To function as rewards, floral nectar and pollen need to be able to compete in a 'floral marketplace' of alternative reward options [1]. But what makes a pollinator perceive a reward as 'better' is not straightforward and is mediated by many aspects of reward complexity as well as pollinators' perceptual biases. In addition to sugars, the non-sugar chemical components of nectar can affect nectar's scent and taste and have post-ingestive effects, all of which can alter pollinators' preferences. Secondary metabolites – such as nicotine [24,25], found in tobacco (*Nicotiana)* nectar, and caffeine, found in citrus (*Citrus)* and coffee (*Coffea*) nectar [25,26] – are preferred at particular concentrations in nectar but are aversive at others [26–29]. For example, bumblebees preferred artificial flowers with a low concentration of nectar caffeine over uncaffeinated or high-caffeine flowers [26]. Preferences for or against nectar compounds can also depend on the chemical context: nicotine was more aversive to honeybees and two species of nectar-feeding birds at lower concentrations of sucrose [27–29]. Similarly, hawkmoths (*Manduca sexta*) preferred solutions containing amino acids at higher sucrose concentrations [30]. Many secondary metabolites also affect preference via effects on physiology and cognition, in addition to, or

Glossary

Associative learning: the formation of a mental connection between representations of two stimuli. In the case of classical conditioning, an initially neutral stimulus (conditioned stimulus, CS) is paired with the unconditioned stimulus (US), which elicits an unconditioned response (UR). Once the association is learned, the CS will elicit the UR without the US being present; the animal has learned that the CS predicts the US.

Cognition: the mechanisms by which animals acquire, process, store, and act on information from their environment [5].

Conditioned stimulus: a stimulus that the animal has no prior response to, that they then learn to respond to in a particular manner after pairing that stimulus with a reward or outcome.

Incentive contrast effects: an exaggerated response of aversion or preference in response to changes in a given reward caused by recent experience with other reward types varying along the same dimension of quality.

Independence from irrelevant alternative: a principle of rational choice theory stating that if an individual chooses option A when given a choice between A and B, they should also choose A if given a choice between A, B, and a less-attractive option, C.

Irrational behavior: behaving in a way that does not maximize expected benefits. This does not imply that certain cognitive or emotional processes are involved in causing such behaviors, but instead focuses on decision outcomes.

Proportional processing: a decision-making process in which an animal compares stimulus values according to their proportional differences. As the overall stimulus magnitude increases, increasingly larger absolute differences in magnitude are needed to elicit behavioral responses.

Secondary metabolites: natural chemicals produced by plants that are not used in primary metabolic pathways.

Transitivity: a principle of rational choice that applies to binary choices and states that if A is preferred to B, and B is preferred to C, then A should be preferred to C (i.e., non-circular preference: A>B>C).

Unconditioned stimulus: a stimulus that unconditionally, naturally, and automatically triggers a behavioral response.

regardless of, their taste. For example, caffeine increases bees' sucrose responsiveness [31], making bees more responsive to lower-quality rewards, meaning that they could perceive a given reward as better than it is. Indeed, many plants not only use neuroactive compounds, but also co-opt insect neurohormones to tap into neural pathways to alter perception (reviewed in [32]). Octopamine, an insect neurohormone found in floral nectar [31], can increase bees' sucrose responsiveness at high concentrations in several species (reviewed in [33]). Interestingly, while octopamine does not seem to have direct effects on bumblebees at field-realistic concentrations (but see [34]), its presence eliminated the effects of caffeine, including on gustatory responsiveness, preferences, and flower visitation rate [31], highlighting the potential for interactive or synergistic effects of nectar chemicals. However, nectar can have hundreds of secondary metabolites. Given this, it will be necessary to use more ecologically realistic nectars, as well as conduct comparative work from the plant perspective (e.g., [35]), if we are to gain insight not only into how complex chemical cocktails affect pollinator behavior [36], but also the floral marketplace itself.

In addition to the complexity presented by nectar alone, pollinators often collect multiple rewards, which can interact to affect preference. For example, bees' aversion to chemically protected pollen is offset by flowers containing nectar [37]. This suggests that one function of nectar could be to overcome the ecological cost of defended pollen. Pollen itself is complex, and pollen preferences can be determined by multiple features, including taste [38,39] and nutritional cues [39,40], fatty acids [41], and larval experience [42]. All of these variables could potentially interact with nectar in interesting ways to influence preference. More broadly, some rewards or reward traits may be more likely to interact to influence a pollinator's perception of a flower as a whole, while others may be more readily dissociated: while bumblebees prefer warmer flowers and higher sucrose rewards, these two parameters can readily be processed independently [43]. Only by considering more floral rewards and their potential interactions will we gain a full understanding of how floral preferences are formed in natural systems.

Should all rewards be preferred? Rewarding pollinators while limiting reward removal

A common assumption is that if a reward is more strongly preferred by a pollinator, it will be beneficial to the plant. Plants, however, must limit and control reward removal to optimize pollen transfer [44]. This often involves making a reward attractive in small amounts, but less tolerable in greater quantities, and may be one function of nectar metabolites. For example, moth and hummingbird pollinators of wild tobacco (*Nicotiana attenuata)* spent less time visiting feeders containing nicotine, but visited feeders more frequently [45]. In addition, nicotine-silenced plants had 70% more nectar removed by pollinators than wild-type plants, indicating that nicotine can limit nectar removal while promoting pollination [45]. Similarly, 'toxic' pollen containing bitter saponins was collected less by bumblebees, but more was transferred to conspecifics [46]. Beyond secondary metabolites, other 'unattractive' reward traits could also serve to boost reproductive success. For example, more consistent nectar rewards are often preferred [47,48], yet plants may benefit by varying nectar production rates among flowers: both hummingbirds (*Selasphorus rufus*) and bumblebees (*B. flavifrons*) depart sooner from flowers that are more variable in their nectar volume, reducing the potential for within-plant selfing [49]. Rewards that are costly from the plant perspective are also well defended: pollen contains more chemical defenses than nectar [13], and we would also expect that within a reward type such as nectar or pollen, species with higher-quality, more costly rewards would be more chemically defended, although this has yet to be tested.

Learning about complex rewards

Bees and other pollinators rapidly learn to associate a variety of floral signals with nectar and pollen, and in doing so, they increase their chances of locating high-quality rewards in the future.

From the plant's perspective, pollinator learning can increase the chances of pollen being transferred to conspecifics (reviewed in [50]). Any variables that increase a pollinator's preference for a reward – be it its scent, taste, or a post-ingestive effect – should increase its value to the pollinator and thus enhance the learned response to associated stimuli [5]. We see this with the simplest measures of reward value: higher concentrations of sucrose lead to higher rates of learning in honeybees and bumblebees [51,52] and sweeter pollen is both preferred by bumblebees and increases the likelihood that they will visit the same flower type [38]. However, even just considering nectar sugars, feedback can happen between the initial preference and the later consequence. Sucrose, glucose, and fructose all reinforce learning in honeybees initially, but only glucose and sucrose lead to robust long-term memory, indicating that a sugar's value is determined post-ingestively as well as via taste [53]. In other cases, reinforcement may only happen via post-ingestive consequences. For example, a pollen fatty acid boosted bumblebees' learning when it was ingested during conditioning, and comparison to control treatments ruled out this being driven by solution preference or salience. Instead, this effect seemed to be caused by post-ingestive nutritional consequences [54] (see also [41]). Secondary metabolites can also alter a pollinator's perception of a reward's value, without altering the reward value itself. Octopamine has consistently been found to lower gustatory responsiveness across several bee species (reviewed in [33]), and in doing so, could boost learning through increasing bees' perception of the reward's value when it is found in nectar. More generally, many nectar chemicals, including caffeine, nicotine, beta-alanine, and γ-aminobutyric acid (GABA), are neuroactive and can enhance learning with or without altering pollinator's preferences for the nectar (reviewed in [32]). For example, honeybees do not prefer solutions containing GABA and β-alanine, but ingesting them boosts learning [55].

Another important component of associative learning is that a specific conditioned stimulus reliably predicts a specific unconditioned stimulus [56]. Accordingly, more variable rewards can be more difficult to learn about: bumblebees show lower rates of learning when nectar is more variable in concentration or volume [47,48,52]. Nectar chemistry can be extremely variable across plants within a species [13], and if this affects taste and/or scent of the reward, learning theory would also predict that this would lead to slower learning. As such, we suggest that plants would produce nectar that is less variable in attributes most salient to pollinators. Interestingly, variability in the delay or probability of receiving a reward often enhances learning [56]. Akin to gambling in humans, this is also the case for honeybees, which showed faster learning when a color was intermittently reinforced [57].

While most learning experiments use a single reward type, animals must often learn about multiple rewards concurrently. In addition to nectar, pollen is readily learned about: bumblebees are more likely to visit artificial flowers of a color on which they previously encountered pollen [58], or higher-quality pollen [59], and these associations can be remembered for up to a week [58]. While it seems that nectar and pollen are classified as different rewards by bees [60], how the value of the flower is encoded may be affected by collecting both at the same time. Immobilized pollen-forager honeybees trained to a scent paired with pollen more rapidly learned that scent when it was later paired with 'nectar' (sucrose), compared with controls [61]. This indicates that pollinators could generalize between reward types as they develop learned preferences for a flower. A dioecious plant offering different rewards between phases could benefit from this, such as the herbaceous annual herb, *Withania aristata,* where male flowers offer only pollen and female flowers only nectar [62]. However, learning about two rewards concurrently can also come at a cost: bumblebees that learned a color discrimination with pollen rewards were impaired when also collecting nectar, even when rewards were on the same flower type (Figure 2). The converse was not true: collecting pollen did not impair nectar learning [63]. These findings indicate that nectar may be a more salient reward than pollen, 'distracting' bees from learning

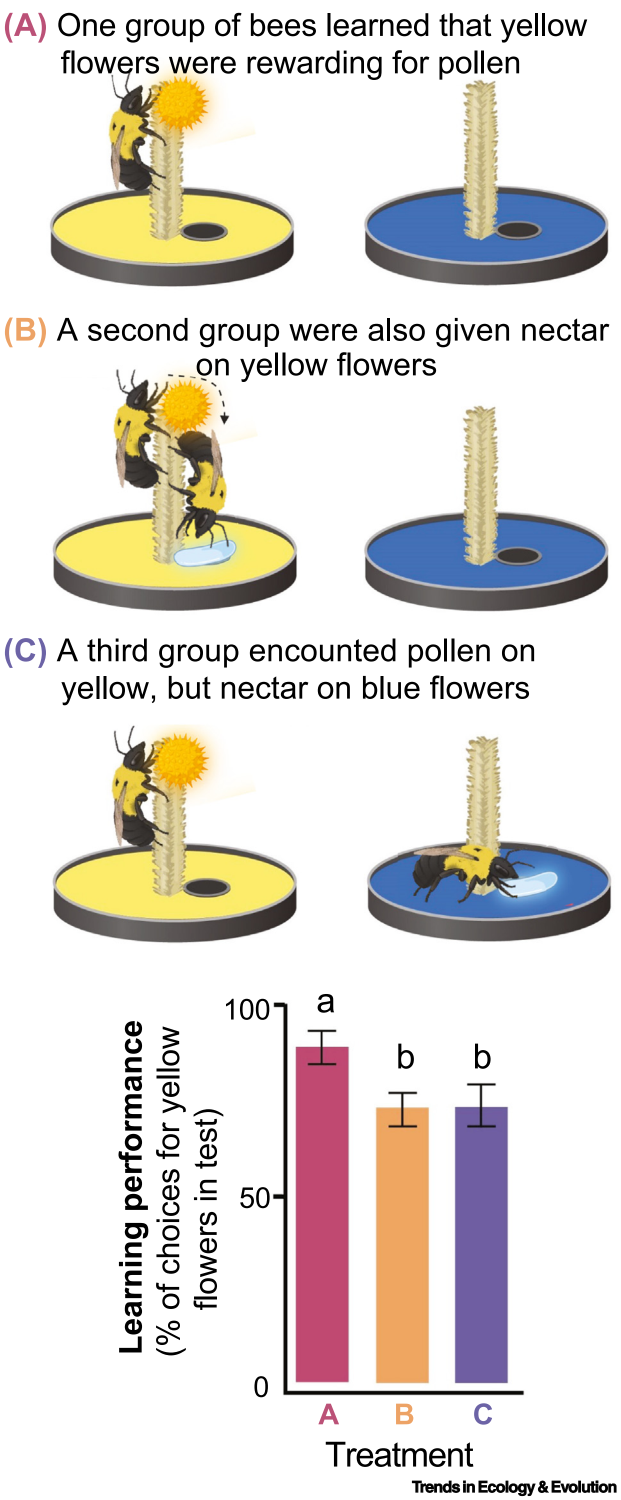

Figure 2. Collecting multiple rewards can impact learning. As part of a larger study, bumblebees were trained to learn that yellow flowers had pollen across three treatments (A, B, and C) with or without nectar. When bees collected nectar (treatments B and C), their ability to learn that yellow flowers contained pollen was impaired, regardless of which flower the nectar was collected from [63]. Results of each treatment are shown in terms of their learning performance (percentage of yellow flowers chosen) in an unrewarded test phase. Letters denote significant differences from each other at $P < 0.05$. It is unlikely that bees' learning performance was impaired because of confusion between different flowers being rewarding for different reward types. Instead, collecting nectar always lowered bees' motivation to collect and learn about pollen. By contrast, collecting pollen did not affect bees' ability to learn associations with nectar rewards (results not shown here).

pollen associations, and lowering motivation to collect pollen (which was also the case in this study). This raises the question of whether by offering nectar to bees, plants not only pay a lower cost to promote fidelity but may also be able to reduce excessive pollen removal via effects on motivation and learning. Work at the neurogenomic level is consistent with pollinators encoding nectar and pollen as distinct rewards [64], although this research involves comparisons of nectar- vs. pollen-foraging honeybees, and whether these results hold within individuals is unknown. A greater understanding of the cognitive mechanisms involved in processing multiple rewards will shed light on how plants may use them to their advantage.

Comparing and evaluating complex rewards

Learning about a flower type and forming a preference does not happen in isolation, but occurs in the context of the other rewards available. As such, reward preferences are subject to pollinators' perceptual biases. Many pollinators prefer higher sugar concentrations in nectar [14], and yet do not always choose the most concentrated option because of how animals perceive differences in magnitude, where values are compared based on proportional rather than absolute differences [65]. This can explain why the concentration of sugar in floral nectar of many species is lower than their pollinators' preferences [66]. While nectivorous pollinators are sensitive to concentration differences (bumblebees [52,67], honeybees [68], bats [69,70]), the relationship between the actual and perceived reward value is logarithmic (similar to 'Weber's law'), meaning that discrimination among nectar concentrations is highest at low concentrations (e.g., 10% is strongly preferred over 5%), but diminishes at higher values (e.g., 35% is not strongly preferred over 30%) [71]. An elegant experiment using wild nectar-eating bats (*Glossophaga commissarisi*) visiting artificial flowers with 'evolving genomes' demonstrated how this perceptual bias can exert stabilizing selection on intermediate nectar values. In this experiment, bats selected for intermediate, rather than the highest, nectar concentrations [69]. Bees and bats also use **proportional processing** when assessing nectar volume [69,72]. Interestingly, when both nectar volume and concentration were manipulated together, bats selected more dilute nectars at lower volumes, suggesting that the evolutionary trajectory of nectar concentration is also influenced by nectar availability [69]. Because increasing nectar quality has diminishing returns in terms of pollinator preference, we suggest that it may pay for plants to move into a new 'reward space' and invest in a different nectar attribute. How magnitude effects play out likely differs among pollinators [71], and may also vary across other reward attributes and types. For example, we would expect stronger magnitude effects with concentration for bees, and volume for bats and birds, since honeybees and bumblebees are relatively better at discriminating between nectars at higher concentrations, reflected in the flowers they visit, with bat- and bird-flowers containing more dilute, higher-volume nectar [71].

For simple nectar proxies (sucrose), it is well established that bees do not evaluate these rewards in absolute terms, but in contrast to recent experience. For example, **incentive contrast effects** can lead to exaggerated responses of aversion or preference: 30% sucrose is perceived as high-value following 15% sucrose, but that same reward may be rejected following experience with 50% [67,68,73]. As such, greater competition between co-flowering species may be reflected in generally higher-quality rewards (e.g., larger nectar volumes [74]), but see proportional processing discussed earlier. Incentive contrast effects in pollinators have only been studied in the context of nectar concentration, but classic work in other systems tells us that contrast effects can occur with disparities in quantity and can be modulated by reward schedule and variation in reward magnitude [75]. As such, we would also expect pollinators to show contrast effects with other nectar attributes and chemical components, especially for traits that can be perceived quickly (e.g., via taste). For example, many female butterflies prefer nectars containing amino acids [76], and as such, they may show contrast between solutions that vary in amino acid composition or concentration. We would also expect incentive contrast to influence acceptance of aversive substances, such as secondary metabolites, leading pollinators to tolerate some amount of bitterness or distastefulness in nectar immediately following more aversive flower types. Beyond nectar, we propose that contrast effects could drive preferences in other rewards, too, such as pollen, especially given that bees taste the pollen they collect [38,39], making short-term assessment possible.

Whether a particular species shows contrast effects in a given context will likely depend both on the reward traits (how much they differ from each other, how easily detectable they are) and on their relative importance to the pollinator in question. As such, we would also expect differences between species. Even just considering nectar concentration, bumblebees and honeybees vary in their incentive contrast response: when a highly rewarding feeder was replaced with a lower quality one, bumblebees rapidly rejected it to search for something better, whereas honeybees were slower to abandon it [77]. In this case, this may be because of differences in foraging strategies between honeybees and bumblebees. Bumblebees' colonies are smaller than honeybees', meaning that the consequences of an individual's foraging decisions may have higher costs. Bumblebees also have a less sophisticated means of communicating, and thus may rely more on individually acquired information [78]. Ultimately, we would expect the strongest selection against trait variability in plant species where their pollinators are most sensitive to differences in that reward trait, although, as previously mentioned, some variability could increase plant fitness by reducing geitonogamy.

Pollinators also need to make decisions between flowers that vary in multiple reward attributes. Nectar and pollen both vary in several aspects of quality, meaning that instead of competing with one another along a single axis, we suggest that flowers may 'escape' competition by investing in a reward on another axis. However, this could result in cases where these attributes are negatively correlated such that there is no best flower type within a patch. In such 'unfriendly' choice environments, animals are prone to economically **irrational behavior**, and typically rely on decision mechanisms based on comparisons between alternatives available [79]. While considered 'irrational' in economic terms, comparative decision heuristics often allow animals to more efficiently exploit variable environments [80]. Although such behaviors deviate from expectations of optimal foraging models [81], irrational or context-dependent decisions appear common across nectivorous pollinators when making decisions between flowers that vary along multiple axes of reward quality and quantity [15]. For example, honeybees violate the economic principle of **transitivity**, showing circular preferences when ranking artificial flowers that vary in depth and volume: bees preferred flower A over B, B over C, C over D, but D over A [82] (Figure 3A). Honeybees, bumblebees, and hummingbirds also commonly violate the principle of **independence from irrelevant alternatives***,* showing evidence for 'decoy effects', where the introduction of a lower-value ('decoy') option changes preference relationships between higher-value options (Figure 3B). Decoy effects occur across a variety of nectar attributes, including concentration, volume, floral depth, and temperature (reviewed in [15]). Pollen also varies along many reward dimensions (e.g., protein, lipids, alkaloids, etc.), and it seems likely that, in some cases, evaluation would vary in context-dependent ways, although this has not been tested. Comparative evaluation can also influence how flowers are remembered for later decisions: when bumblebees learned that flower A was better than B and separately that C was better than D, bees used an 'ordinal ranking' strategy, preferring C to B, even if it was less rewarding in its absolute value [83]. Such findings indicate that both the learning and choice context can affect decision outcomes. Ultimately, we expect ordinal ranking strategies to be especially common when pollinators encode information across multiple value dimensions and where reward quality attributes are positively correlated within a flower type.

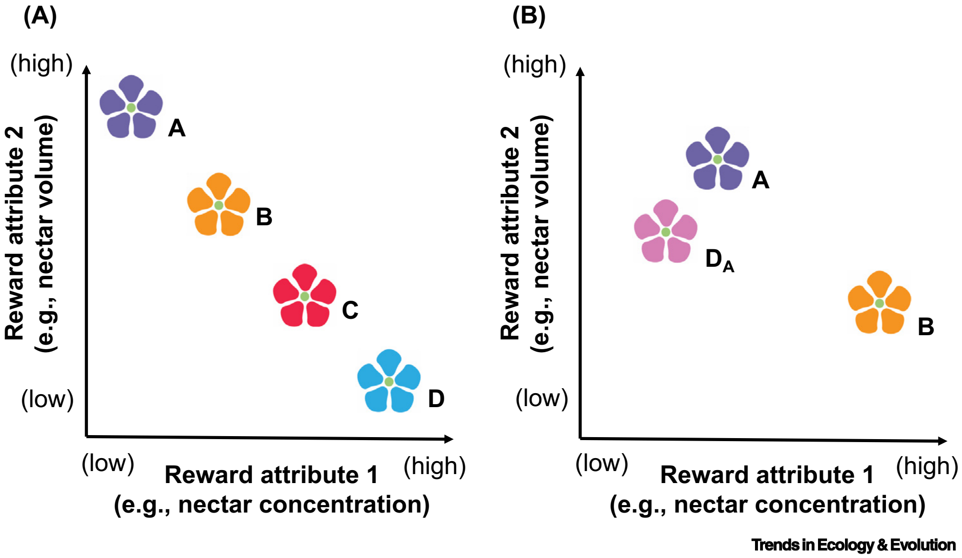

Figure 3. Irrational decision-making with multi-attribute floral rewards. Examples of floral reward attributes that can be involved in (A) transitivity, and (B) decoy effects, causing economically 'irrational' decisions. Intransitive preferences often occur as options become further apart along respective attributes (i.e., A versus D), and when differences along each attribute carry different weightings. 'Decoy' effects typically occur when the decoy (D_A) is worse in two reward attributes than one option (A), but only worse in one than the other (B). In such cases, we would not expect a strong preference between A and B since they trade off in their value across the two reward attributes. However, we often see an increase in preference for flower type A relative to B if option D_A is added.

Generalist pollinators often forage in environments with multiple co-flowering species, and making decisions between flowers is clearly multifaceted, even when just considering nectar. With increasing choice complexity, there may be a greater reliance on comparative decision-making and decision heuristics [84]. Because pollinator choices mediate interactions between flowers within a community, such context-dependent preferences indicate that both high-value and low-value flowers can influence pollinator preferences in ways previously unconsidered [15]. Such findings highlight the importance of incorporating multi-attribute choices and ecologically realistic timescales into choice experiments to better understand pollinator preferences.

Concluding remarks

Complex floral rewards can clearly affect pollinator cognitive performance, and in turn, we argue that understanding cognition can provide new insights into the functional consequences of complex reward phenotypes. Optimal foraging theory laid the foundation for understanding pollinator behavior [85], yet integrating animal cognition and the ecological realism of floral rewards is necessary to fully understand plant–pollinator interactions. Going forward, further incorporating the chemical and ecological complexity of rewards such as nectar and pollen into experiments on pollinator cognition should be a priority (see Outstanding questions). For example, although secondary compounds in nectar have received much attention for effects on behavior when studied in isolation, new work suggests that they may interact with one another to influence several aspects of bee cognition in unpredictable ways [31]. Pollen also has multiple reward dimensions, and despite intense interest in its nutritional value for wild and managed bees, few studies have explored interactions between components of pollen, or how they are evaluated in combination with nectar. At the same time, reward composition and pollinator cognition are each being altered by anthropogenic stressors [86,87], yet these dynamics are only understood in relation to simple floral rewards. Going forward, explicit consideration of how floral rewards comprising multiple

Outstanding questions

Behavioral research investigating the effects of nectar chemistry often addresses phytochemicals in isolation, while real nectar contains many secondary metabolites. What are the potential interactive effects of these chemicals on pollinator cognition?

Cognition is often studied concerning a single reward type; however, animals often collect multiple rewards simultaneously (e.g., nectar and pollen). How are reward perception, learning, and comparative evaluation affected by multiple rewards, in pollinators and more generally?

Most research has focused on nectar and pollen, but plants use other floral rewards too. What cognitive abilities are involved in the collection and assessment of these rewards?

Are similar cognitive abilities convergent in pollinators facing similar ecological challenges, such as evaluating complex rewards, or more universal properties of nervous systems?

Pesticides, pathogens, and global climate change are well established factors that alter floral rewards and influence pollinator cognition, although usually, such work considers a single reward element in isolation. Does the magnitude of these effects change when more complex reward chemistries are considered, or more complex decision scenarios are involved?

Box 1. The stimuli embedded in rewards

In most learning paradigms, conditioned and unconditioned stimuli are decoupled. With floral rewards, however, some stimuli are embedded in the reward as a composite feature. For example, pollen and nectar often contain salient scent [88] and color [1,89,90] cues. While pollinators rely heavily on floral cues when foraging, reward-derived stimuli may be used too.

Many pollinators have strong unlearned preferences for reward-derived stimuli, such as pollen-foraging bees that prefer yellow and UV-absorbing wavelengths. These preferences both match the color of pollen, and appear in other floral features including anthers (Figure IA) and anther- or pollen-mimicking floral patterning (Figure IB) [89,91]. These features are attractive to bees [38,91,92] and difficult for them to learn to avoid [93]. As such, they can be used to 'trick' pollinators into visiting pollen-less female-phase flowers [93]. Many pollinators (especially specialists) likely have innate preferences for pollen [88] and nectar [94] scents too, yet here the influence on preferences may be more complex, with scents emitted from rewards containing some components that are attractive, and others aversive, acting to filter pollinators and limit visitation [45].

In other cases, learning may play a greater role than sensory biases. For example, naïve bumblebees did not discriminate between sterile and fertile pollen in yellow monkeyflowers [*Mimulus guttatus* (syn. *Erythranthe guttata*)] based on scent, but developed a preference for fertile pollen following experience with it [95]. Unlearned preferences and learning can also interact: while bumblebees are capable of learning that linalool scent predicts nectar quality, higher concentrations of nectar linalool also taste aversive, placing an upper limit on this chemical's effectiveness as a reward-derived cue from the plant's perspective [96]. More generally, reward-derived stimuli could be particularly good 'honest signals' of reward presence or quality, given their tight link to rewards [1,94], and given many pollinators' ability to learn these associations [95–97]. However, evidence is mixed on whether rewards have this function, especially concerning nectar scent [96,98]; further investigation across additional species is needed. Given pollen's olfactory saliency, it may be a more reliable honest signal: native pollinators preferred the scent of hermaphrodite over female-phase flowers, driven by anther scent [99].

Reward-embedded stimuli can also modulate other aspects of learning: scent can increase the saliency of nectar, making it easier for bees to learn about flower color [100,101]. In addition, social bees can learn that nectar scents predict food from contacting honey and in the case of honeybees, via trophallaxis [102,103], making nectar's scent also a means of communication.

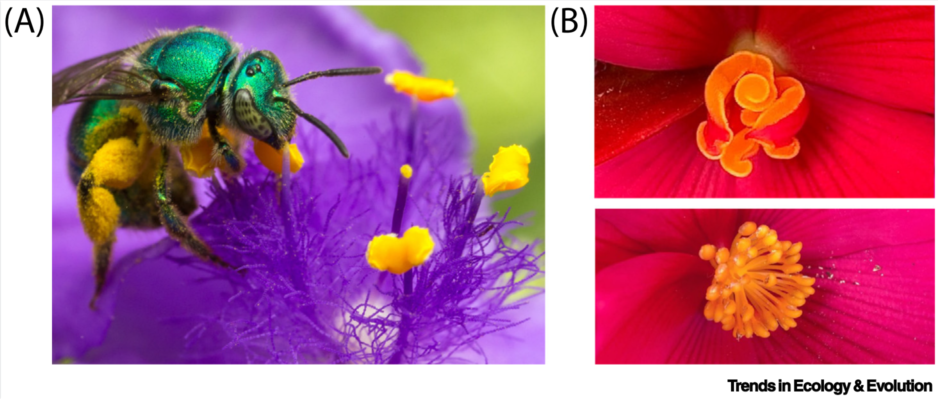

Figure I. Visual signals associated with pollen rewards. (A) A sweat bee (*Augochloropsis metallica*) collecting pollen from a spiderwort (*Tradescantia* sp.). Photo: Alex Wild. (B) *Begonia* flowers, where the stigma of the female morph (upper photo) mimics the stamens of the male morph (lower photo). Photo: Christine DeMarco.

chemicals, attributes, and types can impact cognition will yield a cognitive ecology of pollination grounded in an eco-evolutionary context.

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Declaration of interests

The authors declare no competing interests.

References

1. Raguso, R.A. (2004) Flowers as sensory billboards: progress towards an integrated understanding of floral advertisements. *Curr. Opin. Plant Biol.* 7, 434–440
2. Schiestl, F.P. and Johnson, S.D. (2013) Pollinator-mediated evolution of floral signals. *Trends Ecol. Evol.* 28, 307–315
3. Leonard, A.S. and Masek, P. (2014) Multisensory integration of colors and scents: insights from bees and flowers. *J. Comp. Physiol. A.* 200, 463–474
4. Chittka, L. and Thomson, J.D. (2001) *Cognitive Ecology of Pollination*, Cambridge University Press
5. Shettleworth, S. (2010) *Cognition, Evolution, and Behavior* (2nd edn), Oxford University Press
6. Simpson, B.B. and Neff, J.L. (1981) Floral rewards: alternatives to pollen and nectar. *Ann. Missouri Bot. Gard.* 68, 301
7. Renner, S. (2006) Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In *Plant–Pollinator Interactions: from Specialization to Generalization* (Waser, N.M. and Ollerton, J., eds), pp. 123–144, University of Chicago Press
8. Mithöfer, A. and Boland, W. (2012) Plant defense against herbivores: chemical aspects. *Annu. Rev. Plant Biol.* 63, 431–450
9. Adler, L.S. (2000) The ecological significance of toxic nectar. *Oikos* 91, 409–420
10. Irwin, R.E. *et al.* (2010) Nectar robbing: ecological and evolutionary perspectives. *Annu Re. Ecol. Evol. Syst.* 41, 271–292
11. Stevenson, P.C. (2020) For antagonists and mutualists: the paradox of insect toxic secondary metabolites in nectar and pollen. *Phytochem. Rev.* 19, 603–614
12. Stevenson, P.C. *et al.* (2017) Plant secondary metabolites in nectar: impacts on pollinators and ecological functions. *Funct. Ecol.* 31, 65–75
13. Palmer-Young, E.C. *et al.* (2019) Chemistry of floral rewards: intra- and interspecific variability of nectar and pollen secondary metabolites across taxa. *Ecol. Monogr.* 89, e01335
14. Willmer, P. (2011) *Pollination and Floral Ecology*, Princeton University Press
15. Latty, T. and Trueblood, J.S. (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
16. Pyke, G.H. and Ren, Z. (2023) Floral nectar production: what cost to a plant? *Biol. Rev.* 98, 2078–2090
17. Nicholls, E. and Hempel De Ibarra, N. (2017) Assessment of pollen rewards by foraging bees. *Funct. Ecol.* 31, 76–87
18. Carneiro, L.T. and Machado, I.C. (2023) Oil flowers and related oil-collecting bees: a 50-year timeline of knowledge and future directions. *Arthropod Plant Interact.* 17, 543–562
19. Henske, J. *et al.* (2023) Function of environment-derived male perfumes in orchid bees. *Curr. Biol.* 33, 2075–2080.e3
20. Chui, S.X. *et al.* (2022) Functional resin use in solitary bees. *Ecol. Entomol.* 47, 115–136
21. Schäffler, I. *et al.* (2015) Diacetin, a reliable cue and private communication channel in a specialized pollination system. *Sci. Rep.* 5, 12779
22. Dyer, A.G. *et al.* (2006) Bees associate warmth with floral colour. *Nature* 442, 525
23. Simone-Finstrom, M. *et al.* (2010) Tactile learning in resin foraging honeybees. *Behav. Ecol. Sociobiol.* 64, 1609–1617
24. Baracchi, D. *et al.* (2017) Nicotine in floral nectar pharmacologically influences bumblebee learning of floral features. *Sci. Rep.* 7, 1951
25. Singaravelan, N. *et al.* (2005) Feeding responses of free-flying honeybees to secondary compounds mimicking floral nectars. *J. Chem. Ecol.* 31, 2791–2804
26. Thomson, J.D. *et al.* (2015) Flowers with caffeinated nectar receive more pollination. *Arthropod Plant Interact.* 9, 1–7
27. Köhler, A. *et al.* (2012) Honeybees and nectar nicotine: deterrence and reduced survival versus potential health benefits. *J. Insect Physiol.* 58, 286–292
28. Lerch-Henning, S. and Nicolson, S.W. (2013) Bird pollinators differ in their tolerance of a nectar alkaloid. *J. Avian Biol.* 44, 408–416
29. Gegear, R.J. *et al.* (2007) Ecological context influences pollinator deterrence by alkaloids in floral nectar. *Ecol. Lett.* 10, 375–382
30. Broadhead, G.T. and Raguso, R.A. (2021) Associative learning of non-sugar nectar components: amino acids modify nectar preference in a hawkmoth. *J. Exp. Biol.* 224, jeb234633
31. Muth, F. *et al.* (2022) Discovery of octopamine and tyramine in nectar and their effects on bumblebee behavior. *iScience* 25, 104765
32. Mustard, J.A. (2020) Neuroactive nectar: compounds in nectar that interact with neurons. *Arthropod Plant Interact.* 14, 151–159
33. Muth, F. *et al.* (2023) Octopamine affects gustatory responsiveness and may enhance learning in bumble bees. *Apidologie* 54, 9
34. Barberis, M. *et al.* (2023) Floral nectar and insect flower handling time change over the flowering season: results from an exploratory study. *Acta Oecol.* 120, 103937
35. Manson, J.S. *et al.* (2012) Cardenolides in nectar may be more than a consequence of allocation to other plant parts: a phylogenetic study of *A. sclepias*. *Funct. Ecol.* 26, 1100–1110
36. Parachnowitsch, A.L. *et al.* (2019) Evolutionary ecology of nectar. *Ann. Bot.* 123, 247–261
37. Francis, J.S. *et al.* (2019) Nectar quality changes the ecological costs of chemically defended pollen. *Curr. Biol.* 29, R679–R680
38. Muth, F. *et al.* (2016) Bees use the taste of pollen to determine which flowers to visit. *Biol. Lett.* 12, 20160356
39. Ruedenauer, F.A. *et al.* (2015) How to know which food is good for you: bumblebees use taste to discriminate between different concentrations of food differing in nutrient content. *J. Exp. Biol.* 218, 2233–2240
40. Vaudo, A.D. *et al.* (2020) Pollen protein:lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* 11, 132
41. Ruedenauer, F.A. *et al.* (2020) Best be(e) on low fat: linking nutrient perception, regulation and fitness. *Ecol. Lett.* 23, 545–554
42. Ruedenauer, F.A. *et al.* (2020) Young bumblebees may rely on both direct pollen cues and early experience when foraging. *Proc. R. Soc. B* 287, 20201615
43. Whitney, H.M. *et al.* (2008) The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. *Naturwissenschaften* 95, 845–850
44. Hargreaves, A.L. *et al.* (2009) Consumptive emasculation: the ecological and evolutionary consequences of pollen theft. *Biol. Rev.* 84, 259–276
45. Kessler, D. and Baldwin, I.T. (2007) Making sense of nectar scents: the effects of nectar secondary metabolites on floral visitors of *Nicotiana attenuata*. *Plant J.* 49, 840–854
46. Wang, X.-Y. *et al.* (2019) Bumblebee rejection of toxic pollen facilitates pollen transfer. *Curr. Biol.* 29, 1401–1406.e4
47. Waddington, K. *et al.* (1981) Floral preferences of bumblebees (*Bombus edwardsii*) in relation to intermittent versus continuous rewards. *Anim. Behav.* 29, 779–784
48. Dukas, R. and Real, L. (1993) Effects of nectar variance on learning by bumble bees. *Anim. Behav.* 45, 37–41
49. Biernaskie, J.M. *et al.* (2002) Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar volumes? *Oikos* 98, 98–104
50. Leonard, A.S. *et al.* (2011) Forget-me-not: complex floral displays, inter-signal interactions, and pollinator cognition. *Curr. Zool.* 57, 215–224
51. Loo, S. and Bitterman, M.E. (1992) Learning in honeybees (*Apis mellifera*) as a function of sucrose concentration. *J. Comp. Psychol.* 106, 29–36
52. Cnaani, J. *et al.* (2006) Flower choice and learning in foraging bumblebees: effects of variation in nectar volume and concentration. *Ethol* 112, 278–285
53. Simcock, N.K. *et al.* (2018) Appetitive olfactory learning and memory in the honeybee depend on sugar reward identity. *J. Insect Physiol.* 106, 71–77
54. Muth, F. *et al.* (2018) A pollen fatty acid enhances learning and survival in bumblebees. *Behav. Ecol.* 29, 1371–1379
55. Carlesso, D. *et al.* (2021) Nectar non-protein amino acids (NPAAs) do not change nectar palatability but enhance learning and memory in honey bees. *Sci. Rep.* 11, 11721
56. Domjan, M. (2018) *The Essentials of Conditioning and Learning* (4th edn), American Psychological Association

57. Ishida, M. *et al.* (1992) Acquisition and extinction of a shuttling response in honeybees (*Apis mellifera*) as a function of the probability of reward. *J. Comp. Psychol.* 106, 262–269
58. Muth, F. *et al.* (2016) Bees remember flowers for more than one reason: pollen mediates associative learning. *Anim. Behav.* 111, 93–100
59. Nicholls, E. and de Ibarra, N.H. (2014) Bees associate colour cues with differences in pollen rewards. *J. Exp. Biol.* 217, 2783–2788
60. Muth, F. *et al.* (2015) Colour learning when foraging for nectar and pollen: bees learn two colours at once. *Biol. Lett.* 11, 20150628
61. Nery, D. *et al.* (2020) Pollen reinforces learning in honey bee pollen foragers but not in nectar foragers. *J. Exp. Biol* 223, jeb.230250
62. Anderson, G.J. *et al.* (2006) Reproductive biology of the dioecious Canary Islands endemic *Withania aristata* (Solanaceae). *Am. J. Bot.* 93, 1295–1305
63. Muth, F. *et al.* (2017) Multiple rewards have asymmetric effects on learning in bumblebees. *Anim. Behav.* 126, 123–133
64. McNeill, M.S. *et al.* (2016) Brain regions and molecular pathways responding to food reward type and value in honey bees. *Genes Brain Behav.* 15, 305–317
65. Akre, K.L. and Johnsen, S. (2014) Psychophysics and the evolution of behavior. *Trends Ecol. Evol.* 29, 291–300
66. Pyke, G.H. and Waser, N.M. (1981) The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* 13, 260–270
67. Waldron, F.A. *et al.* (2005) Negative incentive contrast induces economic choice behavior by bumble bees. *Int. J. Comp. Psychol.* 18, 358–371
68. Bitterman, M. (1976) Incentive contrast in honey bees. *Science* 192, 380–382
69. Nachev, V. *et al.* (2017) Cognition-mediated evolution of low-quality floral nectars. *Science* 355, 75–78
70. Nachev, V. and Winter, Y. (2012) The psychophysics of uneconomical choice: non-linear reward evaluation by a nectar feeder. *Anim. Cogn.* 15, 393–400
71. Nachev, V. *et al.* (2013) Weber's law, the magnitude effect and discrimination of sugar concentrations in nectar-feeding animals. *PLoS ONE* 8, e74144
72. Waddington, K.D. and Gottlieb, N. (1990) Actual vs perceived profitability – a study of floral choice in honeybees. *J. Insect Behav.* 3, 429–441
73. Couvillon, P.A. and Bitterman, M.E. (1984) The overlearning–extinction effect and successive negative contrast in honeybees (*Apis mellifera*). *J. Comp. Psychol.* 98, 100
74. Ratnieks, F.L.W. and Balfour, N.J. (2021) Plants and pollinators: will natural selection cause an imbalance between nectar supply and demand? *Ecol. Lett.* 24, 1741–1749
75. Flaherty, C.F. (1982) Incentive contrast: a review of behavioral changes following shifts in reward. *Anim. Learn. Behav.* 10, 409–440
76. Alm, J. *et al.* (1990) Preference of cabbage white butterflies and honey bees for nectar that contains amino acids. *Oecologia* 84, 53–57
77. Townsend-Mehler, J.M. *et al.* (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
78. Sherry, D.F. and Strang, C.G. (2015) Contrasting styles in cognition and behaviour in bumblebees and honeybees. *Behav. Process.* 117, 59–69
79. Shanteau, J. and Thomas, R. (2000) Fast and frugal heuristics: what about unfriendly choice environments? *Behav. Brain Sci.* 23, 762–763
80. Fawcett, T.W. *et al.* (2014) The evolution of decision rules in complex environments. *Trends Cogn. Sci.* 18, 153–161
81. Houston, A.I. *et al.* (2007) Do we expect natural selection to produce rational behaviour? *Philos Trans R. Soc B: Biol. Sci.* 362, 1531–1543
82. Shafir, S. (1994) Intransitivity of preferences in honey bees: support for 'comparative' evaluation of foraging options. *Anim. Behav.* 48, 55–67
83. Solvi, C. *et al.* (2022) Bumblebees retrieve only the ordinal ranking of foraging options when comparing memories obtained in distinct settings. *eLife* 11, e78525
84. Hutchinson, J.M.C. and Gigerenzer, G. (2005) Simple heuristics and rules of thumb: where psychologists and behavioral biologists might meet. *Behav. Process.* 69, 97–124
85. Pyke, G.H. *et al.* (1977) Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* 52, 137–154
86. Gérard, M. *et al.* (2023) Sensory perception and behaviour of insect pollinators under climate change. *Nat. Clim. Chang.* 13, 596–598
87. Richman, S.K. *et al.* (2022) A neonicotinoid pesticide alters how nectar chemistry affects bees. *Funct. Ecol.* 36, 1063–1073
88. Dobson, H.E.M. and Bergström, G. (2000) The ecology and evolution of pollen odors. *Plant Syst. Evol.* 222, 63–87
89. Lunau, K. (2000) The ecology and evolution of visual pollen signals. *Plant Syst. Evol.* 222, 89–111
90. Hansen, D.M. *et al.* (2007) Coloured nectar: distribution, ecology, and evolution of an enigmatic floral trait. *Biol. Rev.* 82, 83–111
91. Heuschen, B. *et al.* (2005) A generalised mimicry system involving angiosperm flower colour, pollen and bumblebees' innate colour preferences. *Plant Syst. Evol.* 252, 121–137
92. Lunau, K. and Maier, E. (1995) Innate colour preferences of flower visitors. *J. Comp. Physiol. A.* 177, 1–19
93. Pohl, M. *et al.* (2008) Anther-mimicking floral guides exploit a conflict between innate preference and learning in bumblebees (*Bombus terrestris*). *Behav Ecol Sociobiol* 63, 295–302
94. Raguso, R.A. (2008) Wake up and smell the roses: the ecology and evolution of floral scents. *Annu. Rev. Ecol. Evol. Syst.* 39, 549–569
95. Haber, A.I. *et al.* (2021) A sensory bias overrides learned preferences of bumblebees for honest signals in *Mimulus guttatus*. *Proc. R. Soc. B* 288, 20210161
96. Burdon, R.C.F. *et al.* (2020) Scented nectar and the challenge of measuring honest signals in pollination. *J. Ecol.* 108, 2132–2144
97. Dobson, H.E.M. *et al.* (1999) Pollen odor chemicals as modulators of bumble bee foraging on *Rosa rugosa* Thunb. (Rosaceae). *Plant Species Biol.* 14, 153–166
98. Knauer, A.C. and Schiestl, F.P. (2015) Bees use honest floral signals as indicators of reward when visiting flowers. *Ecol. Lett.* 18, 135–143
99. Ashman, T.-L. *et al.* (2005) The scent of a male: the role of floral volatiles in pollination of a gender dimorphic plant. *Ecol* 86, 2099–2105
100. Kulahci, I.G. *et al.* (2008) Multimodal signals enhance decision making in foraging bumble-bees. *Proc. R. Soc. B* 275, 797–802
101. Kunze, J. and Gumbert, A. (2001) The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behav. Ecol.* 12, 447–456
102. Gil, M. and De Marco, R.J. (2005) Olfactory learning by means of trophallaxis in *Apis mellifera*. *J. Exp. Biol.* 208, 671–680
103. Molet, M. *et al.* (2009) How floral odours are learned inside the bumblebee (*Bombus terrestris*) nest. *Naturwissenschaften* 96, 213–219