Flower choices and cognitive biases in bumblebees: bee-yond rationality

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Mélissa Armand
aus Tournon-sur-Rhône, France
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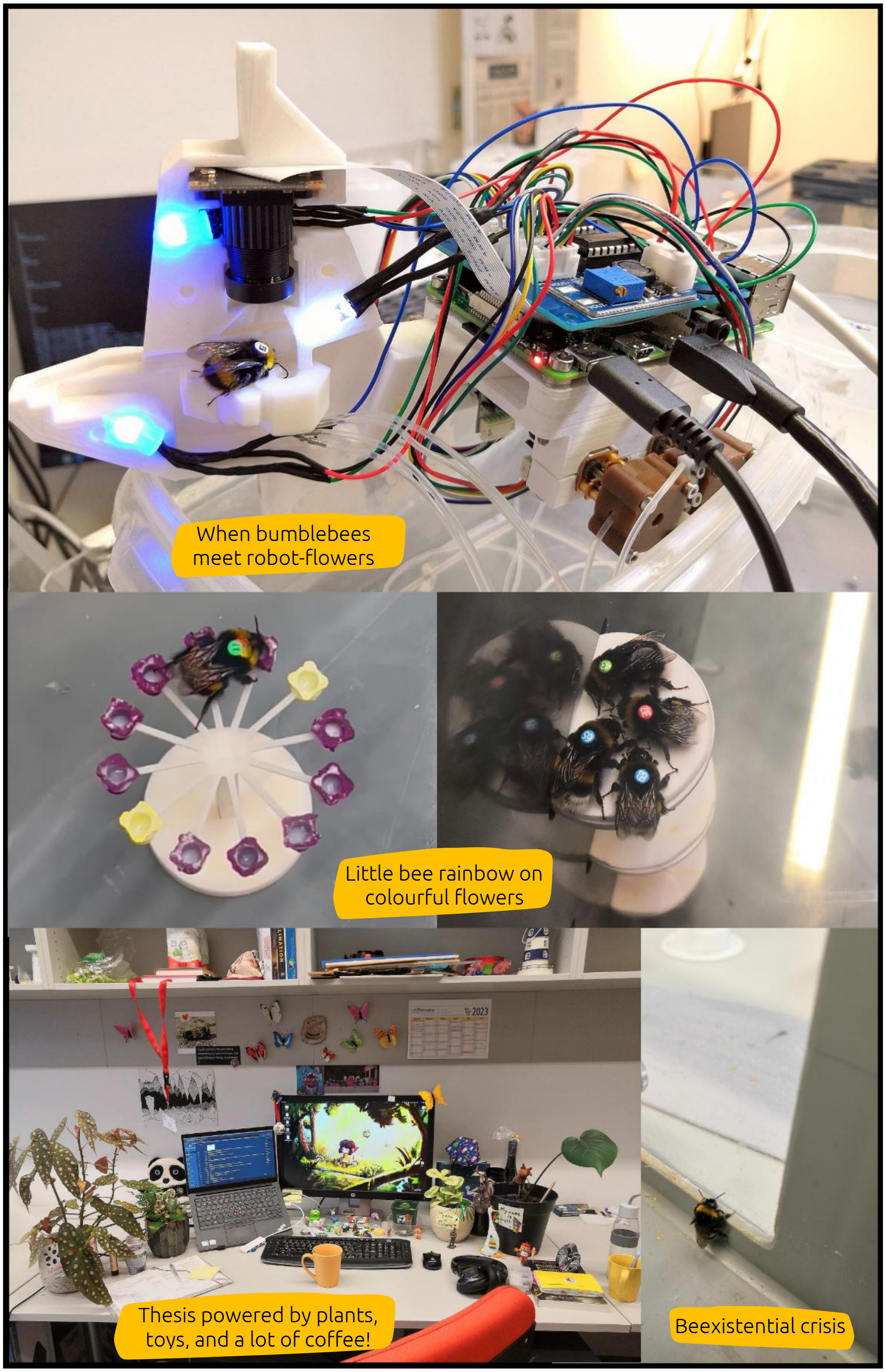
A little photo mosaic illustrating my PhD journey



When bumblebees meet robot-flowers

Little bee rainbow on colourful flowers

Thesis powered by plants, toys, and a lot of coffee!

Beexistential crisis

Table of Contents

Abstract

Bumblebees forage in complex and variable environments, where they must choose among countless flowers that differ in cues and rewards. Although their decisions are often described as rational and efficient, bees frequently face uncertainty and limited information. In such conditions, they may rely on heuristics: simple rules of thumb that help them make good-enough choices under constraints. These shortcuts, however, can give rise to cognitive biases, which are systematic distortions in how options are perceived and evaluated. As a result, bees may make suboptimal or “irrational” decisions that deviate from the predictions of classical economic models. This thesis investigates how individual *Bombus terrestris* foragers perceive and evaluate flowers, and whether their choices are shaped by cognitive biases.

We first examined how individual foraging behaviours emerged. In chapter 1, bees varied in how selective they were toward the sucrose concentration of flower rewards, and in the trade-offs they used to optimise foraging. These differences were shaped by early experiences and environmental conditions. In chapter 2, we asked whether bees’ flower choices were influenced by variability in a neutral cue, focusing on floral scent. Bees showed no preference between flowers with consistent versus variable scent profiles, suggesting that scent variability alone did not strongly influence decision-making. Building on this, chapters 3 and 4 explored whether cognitive biases affected how bees perceived flower value. In chapter 3, we tested the peak-end effect, where a disappointing final reward may reduce the perceived value of an otherwise rewarding flower option. Bees showed no clear peak-end effect but still did not prefer the flower with the highest total reward, likely due to an incentive contrast effect. In chapter 4, we tested the decoy effect, where unrewarding flowers may increase the appeal of neighbouring flowers by contrast. Bees showed no such effect, foraging equally from rewarding flowers and quickly learning to avoid unrewarding ones. In chapter 5, we developed and tested a robotic flower system designed to automate foraging experiments. Bees successfully used the system, demonstrating its potential for high-resolution testing of decision-making and cognitive biases in insect foraging.

Taken together, these findings offer new insight into how individual bumblebees perceive, evaluate, and choose flowers. Across experiments, bees’ decisions reflected context-dependent value perception, influenced by prior experience, environmental conditions, and the available flower options. They also highlight the bounded rationality of bees: individuals relied on simplified decision rules shaped by cognitive and environmental constraints, often deviating from strict economic rationality.

Work arising from this thesis

This thesis comprises four manuscripts, all available as preprints on bioRxiv and submitted for publication in peer-reviewed journals:

A. **Armand M**, Beckenbauer C, Avarguès-Weber A, Lihoreau M, Czaczkes TJ (in revision, *Behavioral Ecology and Sociobiology*) Interindividual variability in flower pickiness by foraging bumblebees

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B. **Armand M**, Zeilmann L, Weinzettl C, Czaczkes TJ (under review, *Insectes Sociaux*) Bumblebees do not prefer consistent floral scents over variable ones

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C. **Armand M**, Riemer P, Hagn S, Schweiger J, Czaczkes TJ (under review, *PLOS One*) Testing the peak-end rule in bumblebees: lack of preference for a higher-reward sequence when the final reward is disappointing

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D. **Armand M**, Herrnberger L, Jung C, Czaczkes TJ (under review, *Ecological Entomology*) No decoy effect in bees: rewardless flowers do not increase bumblebees' preference for neighbouring flowers

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Author contributions

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Mélissa Armand: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Christoph Beckenbauer**: Investigation. **Aurore Avarguès-Weber**: Validation, Resources, Writing - Review & Editing, Supervision. **Mathieu Lihoreau***:* Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing, Supervision, Project administration. **Tomer J. Czaczkes**: Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

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Mélissa Armand: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review and Editing, Visualization. **Lisa Zeilmann:** Investigation. **Christian Weinzettl**: Investigation. **Tomer J. Czaczkes:** Conceptualization, Methodology, Validation, Resources, Writing - Review and Editing, Supervision, Project administration, Funding acquisition.

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Mélissa Armand: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Leonhard Herrnberger:** Investigation, Methodology. **Clara Jung:** Investigation. **Tomer J. Czaczkes:** Conceptualization, Methodology, Validation, Resources, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

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General Introduction

Overview

How bees choose flowers has been a question of interest since the earliest observations of nature. Aristotle, in his *Historia Animalium (*350 BCE), was already pondering the rules behind their flower choices. The remarkable foraging abilities of bees have made them a model of choice for studying foraging behaviour and decision-making (Heinrich, 1979a; Pyke, 1984; Goulson, 1999). Bumblebees, in particular, are highly efficient foragers, visiting up to twenty flowers per minute (Heinrich, 2004). Despite extensive research, bee foraging remains an active area of study, with many open questions. Notably, individual bees differ widely in how they navigate floral environments (Thomson et al., 1997; Saleh and Chittka, 2007; Woodgate et al., 2016), and the mechanisms behind their flower choices are still not fully understood.

Decision-making is central to foraging. Like customers in a marketplace, bees must evaluate and choose between multiple flower options, often under conditions of uncertainty or limited resources. In such contexts, individuals often rely on heuristics, or “rules of thumb”, that simplify decision-making (Simon, 1955; Gigerenzer, 2021). While generally beneficial, heuristics can also lead to systematic errors in judgement, known as cognitive biases (Tversky and Kahneman, 1974). These distortions in value perception often result in suboptimal, “irrational” decisions. Although well documented in humans, the influence of cognitive biases in animal decision-making remains poorly understood (Marsh, 2002), particularly in invertebrates. Yet flower-visiting insects like bees may be particularly prone to such biases, given the unpredictability and complexity of their foraging environments.

This thesis investigates the flower choices of bumblebees through the lens of value perception, focusing on their potential sensitivity to cognitive biases and how these may influence their decision-making. I hypothesise that integrating concepts from behavioural economics into the study of foraging behaviour will enhance our understanding of how bees evaluate and select flowers. Specifically, I examine the foraging behaviour of individual *Bombus terrestris* workers and test whether cognitive biases affect their choices. From a broader perspective, I consider the ecological implications of biased value perception in bee foraging, exploring how heuristics and cognitive biases might affect bee fitness and contribute to the co-evolution of plants and pollinators.

To address these questions, the thesis first investigates how individual foraging behaviours emerge, focusing on the influence of early experiences and environmental conditions (**Chapter 1**). It then examines how neutral cues, particularly scent, affect bee flower choice and the evolution of floral traits (**Chapter 2**). Building on this, it explores whether cognitive biases influence bees’ value perception and flower preferences, focusing on two well-known biases: the peak-end effect (**Chapter 3**) and the decoy effect

(**Chapter 4**). Finally, it presents a prototype of a robotic flower system for studying bee foraging behaviour, and discusses the potential of automation for testing cognitive biases and advancing research on decision-making in insects (**Chapter 5**).

Bumblebees and plant-pollinator relationship

Bumblebees (*Bombus* spp., Hymenoptera, Apidae) are charismatic, highly effective pollinators, representing around 250 species across temperate regions in Europe, Asia and North America (Goulson et al., 2011; Prys-Jones and Corbet, 2015). Most species are generalists, collecting pollen and nectar from a wide range of flowers (Laverty and Plowright, 1988). Their foraging efficiency and high flower visitation rates have made them especially valuable for commercial crop pollination (Velthuis and Doorn, 2006). With their heavy, somewhat clumsy flight, bumblebees have high energy needs and must collect large amounts of nectar (Goulson, 2010). These traits make them ideal for studying individual flower choices.

Most species have an annual life cycle. In early spring, mated queens emerge from hibernation and search for a nest site, often settling in an underground cavity (Goulson, 2010). The queens lay a first batch of eggs which develop through complete metamorphosis, from egg to larva, pupa, and finally adult, until female workers emerge. These workers take over foraging and nest maintenance, allowing the queen to focus entirely on egg-laying. As the colony expands through summer, the queen eventually produces males and new queens. By late autumn, the colony naturally dies off, leaving only the newly mated queens to hibernate through winter and start the cycle anew (Heinrich, 2004).

Bumblebees are considered primitively eusocial, meaning that they display key traits of eusociality but with a simpler social organisation than advanced eusocial insects like honeybees (Cardinal and Danforth, 2011; Sadd et al., 2015). Bumblebee colonies typically consist of 50 to 400 workers (Heinrich, 1979). Unlike honeybees, they don’t perform waggle dances to communicate (Thom et al., 2007). Instead, they likely recruit nestmates by running excitedly and releasing pheromones inside the nest (Dornhaus and Chittka, 1999; 2001), though their communication system is not fully understood.

They exhibit a flexible division of labour (Free, 1955), with workers switching tasks depending on the colony’s needs (Cartar, 1991; Holland et al., 2021). Workers also vary considerably in size (Heinrich, 1979a; Goulson et al., 2002; Spaethe and Weidenmüller, 2002), reflecting the amount of food they received during development (Ribeiro, 1994). Task allocation is mainly based on body size: larger bees tend to forage, while smaller ones care for the nest (Goulson et al., 2002; Jandt and Dornhaus, 2009). Older, more experienced bees often take on pollen foraging, a task requiring greater skill (Raine and Chittka, 2007a; Brito et al., 2010).

B. terrestris as a model organism

Bombus terrestris (Linnaeus, 1758) is an abundant bumblebee species native to Europe and North Africa, and has recently been introduced to various parts of the world due to its extensive commercial use in crop pollination (Ings et al., 2005). Workers of *B. terrestris* are robust and efficient pollinators, collecting pollen and nectar from hundreds of different flower species (Rasmont et al., 2008), and are capable of foraging in temperatures as low as 3°C (Stelzer et al., 2010). Colonies are medium-sized, typically consisting of several hundred individuals (Prys-Jones and Corbet, 2015), and the species can thrive in enclosed environments such as greenhouses and experimental cages (Velthuis and Doorn, 2006). These traits make *B. terrestris* particularly well suited for use in laboratory experiments.

Throughout the experiments described in this thesis, I used *B. terrestris* as a model organism. Colonies were conveniently obtained from a commercial supplier (Koppert) and kept in the lab under controlled conditions. Workers adapted well to free-flying experiments in flight arenas, and their large honey crop capacity (120–180 µL; Lihoreau et al., 2010) enabled the use of visible, measurable sucrose solution rewards. This setup allowed for direct monitoring of flower choices and whether bees collected the rewards during their foraging bouts.

Plant-pollinator relationship

Flowering plants and pollinators form a mutualistic relationship, where each partner provides a service the other cannot perform alone and receives a reward in return (Bronstein, 1994). Plants rely on pollinators to transfer pollen for sexual reproduction, while pollinators depend on plants for food resources. Over 85% of all flowering plant species rely on animal pollination for reproduction, with insects as the main pollinators—and bees as the most important group (Klein et al., 2006; Ollerton et al., 2011). In human-modified landscapes, habitat loss and fragmentation have led to declines in both plant and pollinator populations, disrupting pollination and limiting plant reproduction (Menz et al., 2011). Bees are especially vulnerable, as they depend entirely on flowers for survival, and their global decline in recent decades has been partly attributed to the loss of floral resources (Carvell et al., 2006; Goulson, 2010).

This co-dependent relationship has led to an intricate co-evolution between plants and pollinators, shaped by underlying conflicts of interest between partners (Bronstein et al., 2006). Plants attract pollinators through their flowers, which act like billboards, displaying colours, shapes, and scents to grab their attention (Dobson, 1994), and can adapt and modify these traits to increase their appeal (Raguso, 2008a; Leonard et al., 2011). Bees, in turn, exert selective pressures by favouring certain floral traits, influencing the direction of plant evolution (Goulson, 1999; Harder et al., 2004; Bailey et al., 2007). I discuss how this co-evolution influences bee flower choices in **Chapters 3** and **4**, and how floral scents may evolve in response to bee preferences in **Chapter 2**.

Foraging behaviour

How do bees decide which flowers to visit? Despite decades of research on bee foraging behaviour, the factors driving their flower choices remain surprisingly unclear, with empirical findings often inconsistent or context-dependent. Bumblebees, in particular, show striking interindividual differences in how they explore and exploit floral resources (e.g. Woodgate et al., 2016). This section outlines the main factors shaping bee foraging behaviour, focusing on their preferences and decision-making. Broader external influences, such as predation risk and environmental conditions, are set aside to highlight the internal mechanisms guiding individual choice.

Floral cues

Foraging bees navigate diverse flower arrays rich in multimodal signals (Hebets and Papaj, 2005; Leonard et al., 2012), which they detect and discriminate using their compound eyes, made up of thousands of ommatidia (Meyer-Rochow, 2019). Floral cues play a central role in shaping bee foraging decisions (Chittka et al., 1999; Kulahci et al., 2008; Dunlap et al., 2017). Foragers are initially drawn to flowers by sensory traits like colour, shape, and scent, regardless of the actual reward quality (Orbán and Plowright, 2014a). Naïve bees, with no prior foraging experience, often show spontaneous preferences for certain floral traits—a phenomenon known as innate preference (Heinrich, 1975). These preferences likely evolved through natural selection, as they tend to reflect cues reliably associated with floral quality in natural environments (Gumbert, 2000). **Chapters 1** to **4** explore how innate preferences influence bee choices.

Perhaps the most obvious floral cue influencing bee choice is colour. Bees have trichromatic vision, with photoreceptors sensitive to ultraviolet, blue, and green light (Lunau and Dyer, 2024). As a result, they see red poorly, lacking a red-sensitive photoreceptor (Chittka, 1997; Lunau et al., 2011). Colour plays a major role in flower choice (Spaethe et al., 2001; Morawetz et al., 2013), especially at close range, helping bees decide where—and whether—to land (Lunau and Dyer, 2024). Saliency, or how strongly a flower stands out against its background, also plays an important role in attracting bees (Lunau et al., 1990; Gumbert, 2000; Nityananda and Chittka, 2021). Bee colour preferences are discussed across **Chapters 1**–**4**.

Scent is another key trait bees rely on to choose flowers (Burkle et al., 2020), though it has received far less attention than colour (Fenster et al., 2004; Raguso, 2008b). Floral scent bouquets are complex blends of volatile compounds that vary widely across plant species (Levin et al., 2003; Knudsen et al., 2006). Both the composition and intensity of these scents can influence bee foraging decisions (Majetic et al., 2009; Farré-Armengol et al., 2015; Larue et al., 2016). In **Chapter 2**, I explore floral scent in detail and test how variability in scent affects bees' flower choices.

Flower shape also influences bee foraging choices (Giurfa et al., 1996; Plowright et al., 2011). Bees tend to prefer symmetrical flowers (Free, 1970; Giurfa et al. 1996; Rodríguez et al., 2004), as well as larger flowers and floral patches, which are easier to locate (Makino and Sakai, 2007; Ishii et al., 2008; Spaethe et al., 2001). Bees are also attracted to nectar guides, which are visual patterns on some petals, often visible in the UV spectrum, that help orient them at close range (Koski and Ashman, 2014; Horth et al., 2014).

Floral rewards

Flying is particularly energy-intensive for bumblebees (Combes et al., 2020), requiring them to balance their foraging efforts to meet both their own needs and those of the colony (Cartar and Dill, 1990; Molet et al., 2008; Vaudo et al., 2016; Hendriksma et al., 2019). As a result, choosing the right floral rewards is crucial in their foraging decisions. While many studies have investigated bee preferences for specific nectar concentrations and pollen composition, their flower choices remain far from predictable and often differ between individuals (Pamminger et al., 2019; Hemingway et al., 2024). I review key research on how bees select nectar and pollen rewards in **Chapter 1**.

One key factor behind these individual differences is nectar quality. Bees can detect remarkably small differences in sugar concentration, even as little as 2% (Nachev et al., 2013; Whitney et al., 2008), and distinguish between different sugar levels in nectar (Konzmann and Lunau, 2014; Zhou et al., 2024). But not all bees are equally sensitive to sucrose, and this variation can lead to individuals specialising on rewards of different quality (Page et al., 2006; Riveros and Gronenberg, 2010). **Chapter 1** investigates the factors driving individual differences in foraging behaviour, with a focus on variability in bees' pickiness toward nectar quality.

Foraging range and load capacity also contribute to variation in the behaviour of bees. *B. terrestris*, for example, has been recorded foraging 1–5 km from the nest (Osborne et al., 2008), and the duration of its foraging trips depends on the abundance of resources (Westphal et al., 2006). The amount of nectar and pollen a bee can carry is limited by the size of its honey stomach, or crop size, which scales with body size (Heinrich, 1979a; Goulson et al., 2002b; Greenleaf et al., 2007). However, studies reported mixed findings on whether body size is a reliable predictor of foraging performance (Spaethe and Weidenmüller, 2002; Jandt and Dornhaus, 2014).

Learning and memory

Beyond floral traits and rewards, bee foraging decisions are also shaped by their cognitive abilities, including learning and memory. Bumblebees are fast and flexible learners, capable of forming long-lasting associations between floral cues and rewards after just a few experiences (see review by Sherry and Strang, 2015). In the bee brain, mushroom bodies are considered the cognitive centres for learning, memory, and decision-making (Campbell and Turner, 2010; Giurfa and Sandoz, 2012; Li et al., 2017). The following section explores bee cognition from a behavioural perspective, focusing on how bees make foraging decisions based on observed behaviour rather than underlying brain processes.

Bees can rapidly learn to associate neutral cues with pollen and nectar rewards (Kunze and Gumbert, 2001; Wright and Schiestl, 2009; Raine and Chittka, 2008), even when these cues conflict with their innate preferences (Lunau, 1990; Raguso, 2008a; see results **Chapters 1–4**). Learning is especially effective for multisensory cues, such as combinations of colour, scent, and shape (Gegear, 2005; Kulahci et al., 2008; Leonard et al., 2011). Bees also learn how to handle different flower types to extract nectar more efficiently (Laverty, 1994). However, learning ability varies between individuals and colonies (Raine et al., 2006b; Evans and Raine, 2014). Notably, foraging bees often revisit previously depleted flowers, likely due to memory limitations (Chittka et al., 1999; Goulson, 2000b; Saleh and Chittka, 2006). The implications of revisits and foraging errors for flower choice are addressed in **Chapters 1** and **4**.

Bumblebees rely on both long-term and short-term spatial memory when making flower choices. They can remember the location of landmarks and rewarding flower patches over time (Menzel et al., 1996; Osborne et al., 1999; Osborne and Williams, 2001), and use short-term memory to avoid recently depleted flowers (Redmond and Plowright, 1996). Their choices are also influenced by past experiences, such as the order in which flowers were first encountered (Prabhu and Cheng, 2008; Nityananda and Chittka, 2021) or the quality of previous rewards (Bitterman, 1976; Cresswell, 1990; Townsend-Mehler and Dyer, 2012; MaBouDi et al., 2020b; Hemingway and Muth, 2022). **Chapter 4** explores how prior experience shapes bee decision-making, while **Chapter 3** tests whether preferences are affected by the final reward collected on a flower.

Foraging patterns

How do bees navigate complex floral environments? Building on the influence of floral traits and cognition, this section explores the foraging patterns of bees: how individuals select and visit flowers during their foraging bouts.

One of the earliest observed foraging behaviours in bees is flower constancy: the tendency to repeatedly visit the same type of flower, even when other rewarding options are available (Waser, 1986). This behaviour was noted as far back as Aristotle (Grant, 1950) and Darwin (1876), and is common in bumblebees (Heinrich, 1979; Waddington, 1983a; Gegear and Laverty, 2004). Bumblebees also show high site fidelity, often returning to the same flower patches (Manning, 1956; Thomson et al., 1997; Osborne and Williams, 2001; Cartar, 2004; but see Woodgate et al., 2016). Several factors influence constancy, including reward quality (Grüter and Ratnieks, 2011; Nityananda and Chittka, 2020), past experiences (Makino and Sakai, 2007), and social context, such as the presence of conspecifics (Grüter and Ratnieks, 2011; Keasar et al., 2013). Yet the mechanisms behind this behaviour remain unclear, and its adaptive value is still debated (Goulson, 1999; Gegear and Thomson, 2004; Hayes and Grüter, 2022). I examine the benefits of flower constancy in **Chapter 1**, and its potential role in shaping floral traits in **Chapter 2**.

Optimal Foraging Theory (OFT) provides a framework for understanding how animals make foraging decisions (Charnov, 1976). In nectarivores such as bees, OFT suggests that individuals forage to maximise a currency, typically energy gain per unit time, while balancing various costs and constraints to enhance fitness (Pyke et al., 1977; Heinrich, 1979a; Waddington, 1983; Schmid-Hempel et al., 1985; Harder and Real, 1987). Early studies expanded on this concept and developed theoretical models to describe how bees make economic foraging choices. The most common models are outlined in the next paragraph.

One of the simplest foraging patterns is the nearest-neighbour rule, where bees move to the closest unvisited resource (Anderson, 1983). Bumblebees often follow this pattern, visiting flowers in sequence until the resources are depleted (Saleh and Chittka, 2007; Ohashi et al., 2007; but see Lihoreau et al., 2011). Another model, the near-far search rule (Motro and Shmida, 1995) involves making short flights between rewarding flowers and longer ones when encountering poor flower patches (Pyke, 1978; Heinrich, 1979b; Waddington, 1980; Burns and Thomson, 2006). Bees also exhibit traplining, i.e., visiting flowers in a consistent sequence (Manning, 1956), by establishing stable, repeated routes that maximise rewards while avoiding depleted flowers (Thomson et al., 1997; Makino and Sakai, 2004; Lihoreau et al., 2010). The threshold departure rule (Hodges, 1985) suggests that bees leave a plant once the last flower visited offers less nectar than a set threshold, a pattern widely observed in bumblebees (Pyke, 1978; Cresswell, 1990; Dukas and Real, 1993; Goulson, 2000b; Cartar, 2004). These foraging patterns are explored further in **Chapters 1** and **3**.

Foraging bees cannot optimise everything at once; they must make compromises, or trade-offs, when collecting floral resources. Several trade-offs have been described, including speed versus accuracy (Chittka et al., 2003; Burns and Dyer, 2008), reward value versus foraging effort (Lihoreau et al., 2011; Pattrick et al., 2023), and choosing between novel and familiar food sources (Heinrich, 1979a; Keasar et al., 2013). Individual bees often make different trade-offs, prioritising different foraging “currencies”. This behavioural variability has been shown to benefit the colony by maximising overall foraging success, particularly under variable environmental conditions (Muller and Chittka, 2008; Burns and Dyer, 2008; Holland et al., 2021). **Chapter 1** examines these trade-offs and the potential benefits of individual variation.

Bees can also rely on social cues when foraging, such as the behaviour of conspecifics (Kawaguchi et al., 2006; Smolla et al., 2016; Avarguès-Weber et al., 2018), although bumblebees primarily rely on their own exploration to locate food (Dornhaus and Chittka, 2001). One source of social information is the tarsal hydrocarbon footprints bees leave on flowers, which can signal recent visits and influence the choices of other foragers (Schmitt and Bertsch, 1990; Goulson et al., 2000; Stout and Goulson, 2001). In this thesis, however, I focus on individual flower choices—specifically, how bees perceive their options and make decisions based on personal experience. In all experiments, bees were tested individually to isolate their behaviour from social influences.

While these foraging patterns provide a solid foundation for understanding how bees navigate flowers, they do not fully explain all foraging decisions, many of which appear suboptimal (see next section and results **Chapters 1** and **3**). In complex, heterogeneous environments in particular, bees often deviate from established foraging rules (Lihoreau et al., 2011), and individuals show striking variability in their foraging behaviour, even under similar conditions (Thomson et al., 1997; Saleh and Chittka, 2006; Woodgate et al., 2016; MaBouDi et al., 2020b). In the next section, I build on this foundation by integrating concepts from behavioural economics to explore how bees perceive and evaluate flower options, providing novel insights into the cognitive processes behind their choices.

Decision-making processes

How do bees make flower choices? Classical economic models of decision-making, developed in the mid-20th century, propose that individuals behave as rational agents who evaluate all available options and choose the one with the highest expected utility—that is, the option with the greatest payoff weighted by its probability (von Neumann and Morgenstern, 1944; Luce and Raiffa, 1957; Homans, 1958). Within this framework, rational choice theory defines normative decision-making based on several key principles. Utility maximisation assumes that individuals consistently aim to choose the most rewarding option (von Neumann and Morgenstern, 1944). Transitivity ensures logical consistency: if A is preferred to B, and B to C, then A should also be preferred to C (Arrow, 1951). Regularity, or the Luce axiom, holds that introducing new options should not change preferences among existing ones (Luce, 1959). These principles are intuitively appealing and provide a standard for rational behaviour based on the idea that individuals make consistent, optimal choices.

In practice, however, rational choice models often fall short of capturing the complexity of real-world decision-making (Huber et al., 1982; Tversky and Simonson, 1993; Ariely, 2009). Studies in both humans and nonhuman animals, including insects, have repeatedly shown violations of the rationality principles outlined above (Tversky and Kahneman, 1974; Shafir, 1994a; Shafir and LeBoeuf, 2002). Individuals rarely evaluate all available options or systematically compute probabilities, costs, and consequences (McNamara et al., 2006; Shafir, 1994b; Trimmer et al., 2011). Instead, decisions often rely on a mix of intuition and careful evaluation (Evans, 2008; Kahneman, 2003; see next section).

In particular, the value of an option is rarely absolute; it often depends on the other options available in the choice set (Tversky, 1969; Simonson and Tversky, 1992; Latty and Beekman, 2010; Spektor et al., 2021). Many animals rely on comparative valuation, judging options relative to one another or to reference points (Shafir et al., 2002; Bateson et al., 2003; Lea and Ryan, 2015). As a result, choices are often shaped by the broader decisional context, thereby violating the principle of regularity (Huber et al., 1982; Tversky and

Simonson, 1993; Rosati and Stevens, 2009). Comparative decision-making typically requires less cognitive effort and can be just as effective as absolute valuation (Tversky, 1969; Gigerenzer, 1997; Bateson, 2002). Foraging bees, for instance, navigate complex floral environments where options vary across multiple traits—a context particularly suited to comparative evaluation. In **Chapter 4**, I test whether the addition of irrelevant "decoy" flowers shifts bumblebees' preferences toward specific rewarding flowers.

Heuristics

As an alternative to classical rationality, Simon (1955) proposed the concept of bounded rationality: the idea that individuals face limits in what they can know, consider, and compute. As a result, they often rely on simple decision rules, or heuristics, to make good-enough choices under constraints such as limited time, information, or cognitive resources. These "rules of thumb" simplify complex judgement tasks by selectively ignoring parts of the available information (Tversky and Kahneman, 1974; Hutchinson and Gigerenzer, 2005; Korteling and Toet, 2020). Heuristics are especially useful for making quick, flexible decisions in uncertain environments (Kahneman and Tversky, 1984; Bonabeau et al., 2000).

While the concept of heuristics originated in human psychology (Simon, 1955), animals across taxa have been shown to use rules of thumb to make decisions (Marsh, 2002; Hutchinson and Gigerenzer, 2005; Gigerenzer, 2021). This includes invertebrates, although their decision-making processes remain comparatively underexplored (but see Detrain and Deneubourg, 2002). Examples of heuristics in insects are examined in **Chapters 3** and **5**. Bees, in particular, often rely on simple decision rules when foraging. For example, many of the foraging patterns described in the previous section, such as the nearest-neighbour and near-far search rules, are considered heuristics (Anderson, 1983; Burns and Thomson, 2005). **Table 2** (p. 14) reviews heuristics identified in bee foraging studies.

Heuristics are generally adaptive, often leading to satisfactory decisions (Tversky and Kahneman, 1974; Gigerenzer, 2008; see **Table 2**), particularly in familiar contexts (Goldstein and Gigerenzer, 2002; Gigerenzer and Gaissmaier, 2011). They can even outperform complex optimisation models by relying on limited but relevant information, especially under conditions of uncertainty (Gigerenzer and Todd, 1999; Gigerenzer, 2008). Despite these advantages, much of the literature has examined heuristics through the lens of irrationality and judgement errors (Gigerenzer, 2008). Because they aim for good-enough rather than optimal solutions, heuristics sometimes lead to flawed decisions.

Cognitive biases

Building on Simon's concept of bounded rationality, Tversky and Kahneman (1974) demonstrated through a series of experiments that heuristics often produce consistent biases in judgement, known as cognitive biases. These distortions in how individuals perceive and evaluate options result in flawed or suboptimal decisions, violating the principles of rational choice proposed in classical economic models

(Tversky and Kahneman, 1981; Kahneman and Tversky, 1984; Huber et al., 1982; Shafir and LeBoeuf, 2002). Cognitive biases are systematic and predictable, meaning they are not random errors but occur reliably across individuals and contexts (Kahneman and Tversky, 2000; Shafir and LeBoeuf, 2002).

Like heuristics, cognitive biases have been observed across a wide range of animal species, including invertebrates (Shafir et al., 2002; Bateson et al., 2011; Strang and Muth, 2023). I review insect examples in **Chapter 5**. Cognitive biases often emerge in complex situations where processing capacity is limited and the value of options is misjudged (Kahneman, 2003; Evans, 2008), but they can also arise in surprisingly simple tasks (Tversky and Kahneman, 1981; Huber et al., 1982). These biases tend to be robust, persisting even when decisions are framed differently (Tversky and Kahneman, 1981) or even when incentives or expertise increase (Shafir and LeBoeuf, 2002). Foraging bees, in particular, must often rely on incomplete information, past experiences, or salient floral cues that can distort their perception of reward value, making them especially prone to judgement errors. Cognitive biases in bees are explored in **Chapters 3** to **5**, and **Table 3** (p. 15) reviews those identified in bee foraging.

In animal behaviour research, judgement biases are a type of cognitive bias that describe how internal states influence information processing, leading to seemingly irrational decisions (Harding et al., 2004; Bateson, 2016; d'Ettorre et al., 2017). They are typically studied by observing how individuals respond to ambiguous cues: optimistic individuals are more likely to expect a positive outcome, whereas pessimistic ones tend to anticipate a negative one (Mendl et al., 2009; Strang and Muth, 2023). The effects of optimism and pessimism on decision-making are well documented across species, especially in mammals (see review by Lagisz et al., 2020). Judgement biases have also been studied in insects, including in foraging bees, where they may reflect how internal states shape the perceived value of flower options (see **Table 3**).

Judgement biases are notably used in the context of animal welfare: optimistic biases are typically associated with well-being, while pessimistic ones are linked to negative states such as stress (Harding et al., 2004; Paul et al., 2005; Mendl et al., 2009; Procenko et al., 2024). Similarly, they are increasingly used to investigate emotion-like states in insects—a growing field, though still subject to debate (Solvi et al., 2016; Baracchi et al., 2017b; Chittka and Rossi, 2022). In humans, value perception is often measured through retrospective evaluations or self-reports, methods that are not applicable to other animals. Instead, how animals perceive their options must be inferred from immediate behavioural choices, which can reduce or mask the expression of cognitive biases (see **Chapter 3**). In **Chapter 5**, I explore how automated experimental systems can enhance the detection of cognitive biases in foraging bees.

Rationality and definitions

Rationality is a controversial concept, with its definition varying across disciplines and lacking a unified framework (Kacelnik, 2006). In psychology, rationality is often defined as reason-based, a perspective that may not be well suited to nonhuman animals. In economics, as mentioned earlier, rationality is defined in terms of choice consistency: behaviour is considered rational if it follows a coherent internal logic and satisfies principles such as utility maximization, transitivity, and regularity (von Neumann and Morgenstern, 1944; Arrow, 1986). Biology offers a different view, defining rationality in terms of fitness. From this perspective, behaviour is rational if it enhances reproductive success, even if it appears inconsistent by economic standards (Gigerenzer and Todd, 1999; Marsh, 2002). This view prioritises outcomes over internal coherence (Kacelnik, 2006).

Biologists often combine economic and evolutionary perspectives, linking decision-making processes to fitness outcomes (Kacelnik, 2006; Bateson et al., 2002; Schuck-Paim and Kacelnik, 2002). This thesis builds on that approach by examining deviations from economic rationality in the foraging behaviour of bees, and how these decisions may affect fitness. In the context of foraging, fitness refers to how effectively bees collect resources to support their survival and reproductive success. In the **General Discussion**, I explore how seemingly irrational choices can be ecologically rational and adaptive in some contexts.

Understanding how heuristics, cognitive biases, and rational choice relate to one another can be challenging. Cognitive biases are not always caused by heuristics; they can also arise from learned associations or from the influence of context on perception. Similarly, not all behaviours that appear irrational from an economic perspective result from cognitive biases, although these explain many such deviations (Pronin, 2007). For example, incentive contrast (when a reward is valued differently based on past experience) is neither a cognitive bias nor the product of a heuristic. Instead, it reflects a motivational or emotional response, rather than a distortion in information processing or judgement. Yet, incentive contrast effects still violate the principle of regularity (Luce, 1959), as the same reward can be valued differently depending on prior experience. In this thesis, I explore foraging behaviours in bees that appear economically irrational in a broader sense, whether they are driven by cognitive biases, heuristics, or other mechanisms.

Moreover, there are no clearly established definitions of heuristics or cognitive biases, and their exact meanings and scope remain subjects of ongoing debate (Juan et al., 2021; Acciarini et al., 2021). The list of recognised examples continues to grow and often varies between authors (Ellis, 2018). This lack of a unifying framework makes these processes particularly difficult to identify. To clarify how the terms are used throughout this thesis, I propose the following working definitions and scopes in **Table 1** below.

Table 1: Definitions and distinctions among key decision-making terms

Term	Definition	Implications	Example in bees
Heuristic	Simple decision rule that ignores some information, used to make fast, “good-enough” choices	Often helpful, but can lead to mistakes or suboptimal choices (i.e., any of the term below)	Choosing the nearest unvisited flower as foraging rule
Cognitive bias	Systematic distortion in perception, evaluation, or judgement, leading to predictable deviations from rational choice	Can result from heuristics, but also learning, internal states, attention, memory, or context	Preferring a flower because of a strong first reward, ignoring better overall flower options
Judgement bias	A type of cognitive bias where internal states cause systematic deviations from rational choice	Term from animal behaviour research; often linked to emotional or motivational states	Interpreting an ambiguous cue as negative when stressed, or as positive when motivated
Deviation from rationality	Any behaviour that violates the normative principles of rational choice theory (e.g. consistency, transitivity, regularity, or utility maximisation)	Broader than cognitive bias; includes any departure from rational decision-making, whether biased or not	Rejecting a flower after experiencing a better reward, despite having accepted it before

On pages 14 and 15, I present a comparative overview of heuristics (**Table 2**) and of cognitive biases and other deviations from economic rationality (**Table 3**) observed in foraging bees. These examples were either explicitly identified by the authors or interpreted as such based on the available evidence, with the understanding that some may be open to alternative interpretations. To my knowledge, this is the first comprehensive review of its kind and may provide a valuable foundation for future research on bee foraging behaviour.

Thesis outline and objectives

Bees navigate complex floral environments, often relying on heuristics to make quick and effective decisions. Yet, these shortcuts can sometimes distort their value perception, leading to systematic errors and suboptimal foraging choices. This thesis investigates how individual bumblebees (*Bombus terrestris*) select flowers, examining their sensitivity to cognitive biases and exploring the ecological implications of their decision-making processes.

Chapter 1 examines how early experiences and initial environmental conditions shape individual differences in flower choice, particularly in bees’ selectivity for nectar quality. **Chapter 2** explores how floral traits influence bee preferences, focusing specifically on scent, an often overlooked floral cue, and considers how these preferences may influence the evolution of floral signals.

Chapter 3 investigates cognitive biases in bee decision-making, testing bees' sensitivity to the peak-end effect by examining whether the sequence in which nectar rewards are encountered shapes their flower preferences. **Chapter 4** explores another well-known cognitive bias, the decoy effect, assessing whether the presence of rewardless "decoy" flowers influences bees' perception of neighbouring rewarding flowers.

Finally, **Chapter 5** introduces an automated robotic flower system designed to study bee decision-making. By precisely controlling nectar rewards and floral traits, this system opens new opportunities for detecting subtle cognitive biases and deepening our understanding of how bees evaluate flower options.

By applying concepts from behavioural economics to bee foraging behaviour, this thesis offers new insights into how bees perceive, evaluate, and select flowers. It highlights instances of seemingly irrational decisions and explores their broader ecological significance.

Table 2: Non-exhaustive list of heuristics reported or identified in foraging bee studies

Study	Species	Observed behaviour	Heuristic (if precised)	General decision-rule
Greggers & Menzel (1993)	*A. mellifera*	Stay if last reward was high, shift if low	Win-stay / lose-switch	If-then rule
Chittka et al. (1997)	*Bombus* spp.	Switch to another species after short handling times; stay after long ones	Win-stay / lose-switch	If-then rule
Keasar et al. (2002)	*B. terrestris*	Tend to repeat a flower choice after a reward; switch after no reward	Win-stay / lose-switch	If-then rule
MaBouDi et al. (2020a)	*B. terrestris audax*	Choose the same flower after a reward; switch after no reward	Win-stay / lose-switch	If-then rule
Keasar et al. (1996b)	*B. terrestris*	Longer flights after non-rewarding visits; shorter flights after rewards		If-then rule
Pyke (1982)	*Bombus spp.*	Leave inflorescence after probing a flower with low nectar; stay if nectar volume is high	Threshold departure rule	If-then rule
Hodges (1985)	*B. appositus*	Leave plant after probing a flower with nectar volume below a threshold; stay if volume is high	Threshold departure rule	If-then rule
Cresswell (1990)	*B. bimaculatus*	Depart based on nectar in the last flower; higher nectar reduces chance of departure	Probabilistic departure rule	If-then rule
Kadmon & Shmida (1992)	*Anthophora* & *Eucera* spp.	Depart from plant based on average reward of two last flowers visited	Probabilistic departure rule	If-then rule
Dukas & Real (1993)	*B. bimaculatus*	Do shorter flights after nectar; longer flights after water		If-then rule
Alem et al. (2016)	*B. terrestris*	Repeat string-pulling actions that bring the flower closer; stop when they don't	Trial-and-error	If-then rule
Leadbeater & Chittka (2005)	*B. terrestris*	Visit an unfamiliar flower type if occupied by a conspecific		Social heuristic
Worden & Papaj (2005)	*B. impatiens*	Choose flower colours previously observed being visited by conspecifics		Social heuristic
Kawaguchi et al. (2006)	*B. terrestris*	Choose flowers with conspecifics when unfamiliar with them		Social heuristic
Kawaguchi et al. (2007)	*B. diversus*	Follow conspecifics on unfamiliar flowers; avoid them on familiar ones		Social heuristic
Leadbeater & Chittka (2009)	*B. terrestris*	Prefer flowers with conspecifics when social cues predict reward; ignore when unreliable		Social heuristic
Smolla et al. (2016)	*B. terrestris*	Choose flowers with conspecifics when rewards are highly variable	Copy-when-uncertain	Social heuristic
Romero-Gonzalez et al. (2020)	*B. terrestris*	In a novel foraging context, attend more to demonstrators that previously predicted reward	Copy-when-uncertain	Social heuristic
Alem et al. (2016)	*B. terrestris*	Observe a successful conspecific, then go to and interact with the same flower		Social heuristic
Loukola et al. (2017)	*B. terrestris*	Observe a successful conspecific, then switch to using the closest ball to reach the food		Social heuristic
Goulson et al. (2013)	*Bombus* spp.	Approach flowers where existing robbing holes are located, matching conspecifics' choice		Social heuristic
Dunlap et al. (2016)	*B. impatiens*	Rely on social cues when reliable; switch to personal cue when unreliable		Social heuristic
Baracchi et al. (2018)	*B. terrestris*	Rely on personal cues for easy tasks; copy conspecifics for hard tasks		Social heuristic
Zimmerman (1982)	*Bombus* spp.	Preferentially move to the nearest unvisited flowers	Nearest-neighbour rule	Movement based rule
Pyke (1978)	*Bombus* spp.	Select closest flower within limited angle		Movement based rule
Waddington & Heinrich (1979)	*B. edwardsii*	Move upward and adjust starting and leaving points based on nectar distribution		Movement based rule
Heinrich (1979a)	*B. vagans*	Move upward and adjust starting and leaving points based on nectar distribution		Movement based rule
Pyke (1979)	*B. appositus*	Moves upward between flowers on the inflorescence		Movement based rule
Corbet et al. (1981)	*B. hortorum*	Move upward on raceme after visiting a flower in upright posture		Movement based rule
Corbet et al. (1981)	*B. terrestris*	Rob flowers facing either head up or head-down, then move in the same direction		Movement based rule
Best & Bierzychudek (1982)	*B. flavifrons*	Start at lowest flower, move upward, and leave when reward drops below average	Threshold departure/ bottom-top visitation	Movement based rule
Galen & Plowright (1985)	*B. terricola*	Arrive where rewards are densest (base for nectar, middle for pollen); move upward		Movement based rule
Harder et al. (2004)	*Bombus* spp.	Start visits at bottom flowers of vertical racemes and move upwards consistently		Movement based rule
Heinrich (1979b)	*B. vagans*	Favour the most rewarding flowers; if rewards drop, forage on others to reassess and adjust choices	Majoring minoring	Sampling based rule
Keasar et al. (2002)	*B. terrestris*	Gradually specialise on the higher rewarding flower type while still occasionally sampling the alternative		Sampling based rule
Lotto & Wicklein (2005)	*B. terrestris*	Compare the colours of nearby flowers to identify the rewarding target flower		Perceptual rule
Zhang et al. (2005)	*A. mellifera*	Remember the sample and choose the matching pattern based on its learned location		Perceptual rule
MaBouDi et al. (2020b)	*A. mellifera*	Choose each flower colour with a probability proportional to its past reward experience	Probability matching	Probabilistic rule

Table 3: Non-exhaustive list of cognitive biases and deviations from rationality in foraging bees

Study	Species	Observed behaviour	Bias / deviation (if precised)	General error type
Eckstein et al. (2013)	*A. mellifera*	Favoured colour over spatial location, ignoring more reliable spatial cues in a discrimination task		Heuristic based
Kikuchi & Dornhaus (2018)	*B. impatiens*	Flowers with blue were more easily associated with reward than punishment, causing bees to ignore other colours and treat imperfect mimics as rewarding	Asymmetric learning	Heuristic based
Dyer et al. (2014)	*A. mellifera*	Some bees adopted a "stay rule": remained loyal to the colour they initially learned, even when it became unrewarding		Heuristic based
Waddington & Heinrich (1979)	*B. edwardsii*	Persistently moved bottom to top on vertical inflorescences, even when rewards were artificially reversed with highest at the top		Heuristic based
Corbet et al. (1981)	*B. hortorum*	Consistently moved upward on vertical inflorescences even when nectar rewards increased downward		Heuristic based
Dittmar et al. (2014)	*B. terrestris;* *A. mellifera*	Consistently selected corners based on local colour pattern similarity in a homing task, leading to systematic errors; instead relied on external visual cues when available		Heuristic based
Benard & Giurfa (2004)	*A. mellifera*	Failed to choose B over D in a transitive inference task, despite B having higher reward; choices were biased by the most recent reward	Recency effect	Memory based
Schmid-Hempel (1986)	*A. mellifera*	Flight direction was strongly influenced by the most recent reward, even when earlier flowers offered better rewards	Recency effect	Memory based
Prabhu & Cheng (2008)	*A. mellifera*	Preferred the most recently rewarded odour, even though an earlier odour had received more total rewards	Recency effect	Memory based
Nityananda & Chittka (2021)	*B. terrestris*	Preferred the most recently learned flower, even when it had lower reward than the alternative flower option	Recency effect	Memory based
Solvi et al. (2022)	*B. terrestris*	Preferred lower-reward flowers if they had higher remembered rank; relied on ordinal ranking of past options, not absolute reward values, when choosing between novel pairings		Memory based
Zhou et al. (2024)	*B. terrestris*	Training with delayed rewards led to persistent waiting and overgeneralisation of reward timing to novel, unrewarded flower colours		Memory based
Hemingway & Muth (2022)	*B. impatiens*	Generalised reward expectations from trained colour to similar ones, leading to rejection of previously accepted rewards	Label-based expectation	Memory based
Leadbeater & Chittka (2009)	*B. terrestris*	Continued to prefer flowers with conspecifics even when social cues no longer predicted reward, following prior association		Social based / memory based
Dunlap et al. (2016)	*B. impatiens*	Preferred social cues over personal ones even when social cues were less reliable predictors of reward		Social based
Avarguès-Weber et al. (2018)	*B. terrestris*	Continued visiting flowers occupied by conspecifics even when these offered lower rewards than identical unoccupied flowers	Social attraction	Social based
Wiegmann et al. (2003)	*B. impatiens*	After a reward downshift, bees disrupted feeding and were more likely to switch to a novel flower colour, even though both flowers offered the same reward	Negative incentive contrast	Valuation based
Bitterman (1976)	*A. mellifera*	Rejected 20% sucrose after experiencing 40%, despite previously accepting it	Negative incentive contrast	Valuation based
Waldron et al. (2005)	*B. impatiens*	Rejected 20% sucrose after prior exposure to 50%, despite previously accepting it; switched to novel flower options instead	Negative incentive contrast	Valuation based
Townsend-Mehler et al. (2011)	*B. impatiens*	Rejected downshifted sucrose concentrations and searched for novel flowers, despite previously accepting same rewards	Negative incentive contrast	Valuation based
Townsend-Mehler & Dyer (2012)	*B. impatiens*	Previously accepted 0.25 M sucrose was rejected after brief exposure to 2.5 M; bees probed but did not feed	Negative incentive contrast	Valuation based
Hemingway & Muth (2022)	*B. impatiens*	Rejected 30% sucrose more strongly when paired with a familiar colour previously linked to 50% reward	Negative incentive contrast	Valuation based
Banschbach (1994)	*A. mellifera*	When reward differences are subtle, learned colour associations bias bees to choose lower-value options		Valuation based
Skorupski et al. (2006)	*A. mellifera*	Made faster but less accurate decisions when error costs were low, leading to reduced foraging efficiency		Valuation based
Bateson et al. (2011)	*A. mellifera*	Classified ambiguous odours as predicting punishment more often after being stressed (physically agitated)	Pessimism	Judgement bias
Schlüns et al. (2017)	*A. mellifera*	Classified ambiguous odours as predicting punishment more often after being shaken to simulate predator attack	Pessimism	Judgement bias
Perry et al. (2016)	*B. terrestris*	Took less time to approach ambiguous cues and resumed foraging faster after simulated predator attack following unexpected reward	Optimism	Judgement bias
Strang & Muth (2023)	*B. impatiens*	More likely to visit ambiguous colours after receiving an unexpected reward, compared to controls	Optimism	Judgement bias
Perry & Barron (2013)	*A. mellifera*	Opted out more on hard trials, avoiding quinine punishment but missing out on possible rewards		Judgement bias
Perry & Barron (2013)	*A. mellifera*	Transferred opt-out behaviour to novel tasks, avoiding choices even without known difficulty		Judgement bias
Greggers & Menzel (1993)	*A. mellifera*	Visited feeders in proportion to their reward rates rather than maximising; overvisited low-reward feeders and undervisited high-reward ones		Probability fallacy
MaBouDi et al. (2020)	*A. mellifera*	Matched colour choices to the frequency of past rewards for each option, rather than always choosing the most-rewarding one	Probability matching	Probability fallacy
Howard et al. (2017)	*A. mellifera*	Perceived identical-sized targets as different depending on surrounding shapes; showed size illusion under unrestricted but not restricted viewing	Delboeuf illusion	Perception based
Austin et al. (2018)	*B. impatiens*	Became more selective in complex arrays with more flower types, often sticking to one option even when only moderately rewarding	Paradox of choice	Context based

Chapter 1 – Interindividual variability in flower pickiness by foraging bumblebees

Mélissa Armand[1], Christoph Beckenbauer[1], Aurore Avarguès-Weber[2], Mathieu Lihoreau[2] and Tomer J. Czaczkes[1]

[1] Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

[2] Research Center on Animal Cognition (CRCA), Center for Integrative Biology (CBI); CNRS, University Paul Sabatier – Toulouse III, France

Abstract

Pollinators navigate complex and heterogeneous "flower markets", where floral resources vary in quality, availability, and distribution. Bumblebees, as generalist foragers, visit numerous flowers during their foraging bouts. Yet, the factors influencing their flower choices and the notable individual differences in foraging behaviour among bees are still not well understood. We hypothesised that early foraging experiences influence bees' subsequent flower choices. To test this, we observed individual *Bombus terrestris* workers forage for three consecutive bouts in two artificial flower arrays. One array simulated a favourable environment with patches alternating high- and low-quality flowers (40% vs. 20% w/w sucrose solution), while the other array presented a more challenging environment with patches of high-quality flowers alongside unrewarded flowers (40% w/w sucrose solution vs. plain water). In both arrays, bees rapidly improved their foraging efficiency, increasing sucrose intake per unit time across bouts. In the favourable array, most bees became highly selective for high-quality flowers, while some continued visiting both flower types. Their degree of pickiness was influenced by early experiences: bees initially exposed to high-quality flowers became more selective, whereas those encountering low-quality flowers first were less selective in subsequent foraging. Despite differences in pickiness and array conditions, bees achieved comparable sucrose intake rates within three bouts. This study highlights the adaptability of bee foraging behaviour and emphasizes the role of early foraging experiences in driving individual differences.

Significance statement

To forage efficiently, pollinators must navigate complex "flower markets", where floral resources vary in quality and availability. We observed *Bombus terrestris* workers forage across three bouts in two artificial flower arrays: a favourable array with flower patches alternating high- and low-quality flowers (40% vs. 20% w/w sucrose solution), and an extreme array with high-quality and non-rewarding flowers

(40% w/w sucrose solution vs. plain water). We found that bees initially exposed to high-quality flowers became highly selective, whereas those encountering low-quality flowers first were less picky, collecting both flower types. Despite these differences, bees rapidly improved foraging efficiency over successive bouts, achieving similar sucrose intake rates within three bouts. This study highlights the foraging flexibility of bumblebees and suggests that early experiences can have lasting effects, influencing flower choices dozens of visits later.

Introduction

Pollinators such as bees, bats, and birds forage in highly diverse and dynamic "flower markets", where optimising food collection is a complex task. Optimal Foraging Theory (OFT) posits that animals forage in ways that optimise net energy gain, i.e., by maximising energy return per unit of time spent foraging (Pyke, 1984; Schmid-Hempel et al., 1985; Pyke and Starr, 2021). There is no single method for enhancing foraging efficiency across heterogeneous environments: whether by increasing speed, improving accuracy, or maximising nectar volume or quality. Bumblebees are highly efficient central-place foragers, playing a crucial role in pollinating both wild plants and agricultural crops (Velthuis and Doorn, 2006). With a visit rate of 10 to 20 flowers per minute, they can visit several hundreds of flowers daily (Heinrich, 1979a). Notably, considerable interindividual variability has been observed in how bees exploit their environment (Woodgate et al., 2016). Despite extensive research on bee foraging behaviour (see review by Sommer et al., 2022), the factors driving these individual differences remain poorly understood. Early foraging experiences and initial environmental conditions likely play a key role in shaping foraging behaviour. However, why some bees initially accept or reject flowers of varying quality, and how these early choices influence subsequent foraging, remain unclear.

Natural environments are highly dynamic, with nectar availability and quality fluctuating across flowers and throughout the day (Goulson, 2003). For example, aging flowers can alter nectar rewards and change colour (Weiss, 1991; Willmer, 2011). Furthermore, many flowers lack nectar entirely, with up to 70% on a single plant being nectarless (Real and Rathcke, 1988; Cresswell, 1990; Thakar et al., 2003). Nectar quality also varies greatly, with sugar concentrations ranging from 10% to 80% w/w (Kevan and Baker, 1983). Additionally, individual bees face internal constraints that affect their foraging behaviour. For instance, wing wear can lead bumblebees to favour denser floral patches to minimise flight distances (Foster and Cartar, 2011). Bumblebees differ significantly in size, impacting the amount of nectar they can carry and their overall foraging success, with larger bees showing higher foraging rates (Heinrich, 1979a; Goulson et al., 2002; Spaethe and Weidenmüller, 2002). Experience further shapes foraging, as more experienced bees make more direct and efficient flights (Osborne et al., 2013; Woodgate et al., 2016), although learning ability varies between individuals (Evans and Raine, 2014). Given the high energetic needs of foraging (Darveau et al., 2014; Vaudo et al., 2016), bees must carefully navigate these constraints to maximise efficiency.

Foraging bees typically collect nectar from more than one flower type throughout their lives (Hagbery and Nieh, 2012; Russell et al., 2017), and their floral choices are highly variable across environments and individuals. Naive bees, for instance, often show innate preferences for violet or blue flowers (Gumbert, 2000; Raine and Chittka, 2007), larger flowers, which are easier to locate (Ohara and Higashi, 1994; Spaethe et al., 2001), and large flower patches (Makino and Sakai, 2007). Bumblebees also exhibit flower constancy (the tendency to forage predominantly on a single flower species; Chittka et al., 1999), though they do so more flexibly than honeybees (Osborne and Williams, 2001; Gegear and Laverty, 2004). However, both innate preferences and constancy can be overridden with experience (Gumbert, 2000; Makino and Sakai, 2007). While bees generally prefer higher sugar concentrations (Whitney et al., 2008), they do not always choose nectar-rich flowers. For instance, Abrol (2006) showed that honeybees favoured plants with high flowering density and lower nectar concentration over patches with fewer, nectar-rich flowers. Furthermore, Frasnelli et al. (2021) observed that smaller-size bumblebees invested equal effort in memorising flowers with high and low sugar concentration. Preferences for nectar volume have received less attention, and findings are inconsistent (see: Menzel and Erber, 1972; Waddington and Gottlieb, 1990; Lihoreau et al., 2011). Nonetheless, bees appeared more responsive to changes in nectar concentration than volume (Cnaani et al., 2006). In addition to these factors, floral choices are influenced by the specific energetic needs of bees, as they adjust their foraging behaviour to meet both their individual needs and those of their colony (Molet et al., 2008; Vaudo et al., 2016; Hendriksma et al., 2019).

Depending on environmental conditions, bees may employ various foraging "tactics" to efficiently navigate floral resources. In simpler flower patches, they often follow a nearest-neighbour rule, moving sequentially to the closest unvisited flower until resources are depleted (Saleh and Chittka, 2007; Ohashi et al., 2007). In denser or aggregated patches, bees switch to a near-far search strategy, staying longer in nectar-rich areas and making short flights between rewarding flowers (Heinrich, 1979b; Dukas and Real, 1993), and leaving quickly or taking longer flights when resources diminish (Pyke, 1984; Chittka et al., 1997; Cartar, 2004). In larger-scale environments, bees alternate between exploration and exploitation flights to establish foraging routes (Kembro et al., 2019). They often employ traplining: following fixed routes to maximise rewards while avoiding revisited, depleted flowers (Ohashi et al., 2007; Lihoreau et al., 2010). These routes are gradually refined through iteration, balancing shorter paths with prioritising high-reward flowers (Reynolds et al., 2013). However, foraging patterns in heterogeneous environments are inconsistent (Lihoreau et al., 2012), with individual bees showing marked differences in patch fidelity, the balance between exploration and exploitation, and the duration and frequency of foraging bouts (Woodgate et al., 2016). How bees navigate complex environments is still not well understood.

Here, we conducted a lab-based experiment to investigate how bees improve their foraging efficiency in heterogeneous flower markets. We examined how the quality difference between good and poor flowers within patches influences the foraging behaviour of *Bombus terrestris* workers. Individual bees foraged for three consecutive bouts in two distinct artificial flower arrays. The first array simulated a favourable environment, with patches containing high- and low-quality flowers, alternating ("High vs. Low" array; 40% vs. 20% w/w sucrose solution). The second array represented a more challenging environment, with patches offering a single rewarding flower type alongside unrewarded flowers ("High vs. Water" array; 40% w/w sucrose solution vs. plain water). We hypothesized that early foraging experiences and environmental conditions would shape the bees' subsequent foraging behaviour. Specifically, we predicted that the more extreme conditions in the High vs. Water array would allow bees to learn flower quality more quickly and improve foraging efficiency faster than the bees in the High vs. Low array. Nevertheless, we predicted that bees in both flower arrays would increase their energy gain per unit time over successive bouts, consistent with optimal foraging theory (Pyke, 1984; Schmid-Hempel et al., 1985).

Material and Methods

Bees

Four commercial *B. terrestris* colonies (Koppert, The Netherlands) were maintained under controlled laboratory conditions (22–24°C, 14:10 light:dark cycle; lights on from 6:30 a.m. to 8:30 p.m.) with ad libitum pollen. Colonies were housed in wooden nestboxes, each connected to its respective flight arena (60 x 50 x 35 cm) through a transparent tube fitted with shutters (see apparatus in **Fig. 1**). Between experimental sessions (i.e., pre-training), bees had unrestricted access to six artificial flowers in the arena. Each flower provided ad libitum 20% w/w sucrose solution through a damp cotton mesh soaked in solution and protruding through a central hole. Bees that foraged regularly were individually marked on the thorax with uniquely coloured, numbered tags and selected for the experiment. A total of 52 bees from four colonies were tested over a 20-day period in October–November 2021 (see **Supplement S1** for further colony details). Additionally, six bees from two other colonies were tested in January 2024 in a complementary experiment, to determine whether bees collected the entire sucrose solution drop from the artificial flowers or only part of it. This experiment mirrored the main setup but reversed the flower colours and included weighing the flowers before and after each foraging bout. Results showed that bees typically either fully collected the sucrose drop or rejected the flower without drinking (see **Supplement S2** for detailed analysis).

Artificial flowers

Each flower consisted of a transparent plastic cup (diameter = 38 mm, height = 70 mm) topped with a coloured laminated paper disk. The flowers used during the experiment were either blue (with a peak reflectance at approx. 450 nm) or yellow (with a peak reflectance from approx. 530 to 700 nm, see

Supplement S3 for reflectance curves). Sucrose solution was pipetted onto a small white dot in the centre of each flower, to aid the bees in locating rewards (Heuschen et al., 2005; see **Fig. 1** below). During pre-training, the artificial flowers were made of two halves, one blue and one yellow, following the method of Raine and Chittka (2008). These bicoloured flowers ensured that the bees could associate sucrose rewards equally with each flower colour, which we later used as separate flower types in the experiment.

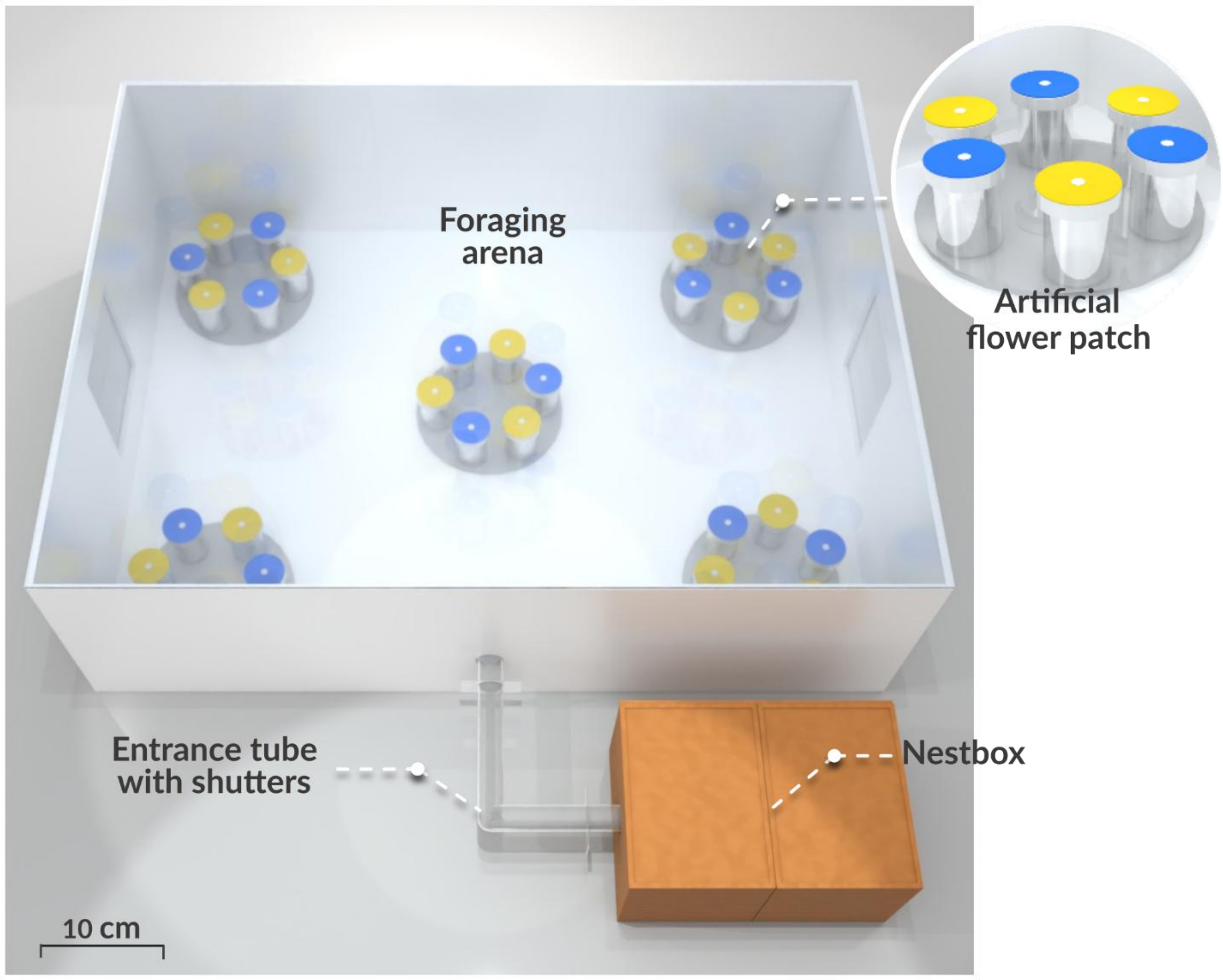

Figure 1: Top view of the scaled experimental setup. The 3D model, created in Blender, illustrates layout pattern A of the flower array (see **Supplement S4** for all layout patterns). Flower patches were positioned 15–50 cm from the arena entrance and mounted on transparent white, circular plastic bases (15 cm diameter, 0.5 cm thick), with flowers within each patch spaced 1.5 cm apart. The flowers were removed and rearranged after each foraging bout using the arena's side doors.

Experiment

Individual bees performed three consecutive foraging bouts to a flower array consisting of five blue/yellow dimorphic flower patches. Each patch contained six flowers arranged in a circle, with alternating blue and yellow flowers ensuring that neighbouring flowers were always of different colours. The patches were arranged pseudo-randomly in an all-white arena using four different layout patterns (see **Supplement S4** for layout patterns). This design ensured that each new foraging bout presented a novel foraging array, preventing the bees from relying on spatial memory from previous bouts. In the main experiment, yellow flowers consistently offered high-concentration sucrose solution to counteract bees' innate preference for blue (as cited in Gumbert, 2000) and to prevent a bias toward blue flowers. To further reinforce the robustness of our setup, the colour assignments were nonetheless reversed in the complementary experiment. The bees were tested on one of two different flower arrays:

(1) High vs. Low flower array (N = 37 bees): For 31 bees, yellow flowers contained 14 μL of concentrated sucrose solution (40% w/w), and blue flowers contained 14 μL of diluted sucrose solution (20% w/w). For the remaining six bees in the complementary experiment, the colours were reversed. This array simulated a favourable environment, with neighbouring flowers offering varying nectar quality. We expected bees in this array to be less selective in their flower choices and to show a slower improvement in foraging efficiency compared to the extreme array described below.

(2) High vs. Water flower array (N = 15 bees): Yellow flowers contained 14 μL of concentrated sucrose solution (40% w/w) and blue flowers 14 μL of plain water. This array represented an extreme environment, with only one rewarding flower type and half the flowers offering no reward. We expected bees in this array to be highly selective and to rapidly improve their foraging efficiency.

In both flower arrays, each flower type provided enough sucrose solution (210 μL per bout) for a bee to fill its crop by visiting a single flower type. This volume exceeds the average crop capacity of bumblebee foragers (120–180 μL; Lihoreau et al., 2010). To prevent chemical marks from influencing flower choices, all flower surfaces were wiped clean with paper towel moistened with 70% ethanol after each bees' foraging bout (Goulson et al., 2000; Saleh et al., 2007).

After the third foraging bout, the bees completed a "test" bout in which the arena contained two monochromatic flower patches, one yellow and one blue, both unrewarded (plain water). The patches were positioned against the back wall, facing the arena entrance, and the bee's first flower visit was recorded as an indicator of its flower type preference.

Data collection

Each foraging bout was video-recorded using a camera (Sony HDR CX405) placed above the flight arena. Bee behaviour was analysed using an event-logging software (BORIS, v8.6), recording: (1) foraging bout durations (i.e., time from entering the arena to returning to the nest), (2) flower visits (bee landing on a flower), (3) flower revisits (bee landing on a previously visited flower within the same bout), and (4) reward collection (bee licking a drop of sucrose solution for over five seconds). Based on video analysis, we considered the bees to either reject, or accept and fully consume the sucrose drop on visited flowers (see **Supplement S5** for video examples). This categorisation was further validated in the complementary experiment, where flowers were weighed before and after each foraging bout (see **Supplement S2** for methodology and results). Bees that accepted a flower overwhelmingly consumed the entire drop, regardless of whether it was high- or low-concentration.

Data analysis

Data processing was performed with Python (v3.11, Python Software Foundation, 2023) using the following libraries: *pandas* (McKinney, 2010) for data structuring, *seaborn* (Waskom, 2021) and *Matplotlib* (Hunter, 2007) for data visualisation, and *Scikit-learn* (Pedregosa et al., 2011) for data clustering. Statistical analyses were carried out with R (v4.1, R Core Team 2022) using the packages *glmmTMB* (Brooks et al., 2017) for Generalised Linear Mixed Models (GLMM), and *emmeans* (Lenth, 2020) for post-hoc tests. Model residuals were evaluated using the *DHARMa* package (Hartig, 2020). The datasets from the main experiment and the complementary experiment, where flower colours were reversed, were merged for analysis. The type of experiment (main or complementary) was included as a random effect to control for potential differences in experimental conditions. Individual bees were also treated as random effects, nested within their respective colonies, to account for variations within colonies. Complete statistical analyses and datasets are available on Zenodo (https://doi.org/10.5281/zenodo.14524634).

(A) Bee clustering

To assess bee pickiness for high-quality flowers in the High vs. Low flower array (see results below), we performed a Principal Component Analysis (PCA) on three key variables from the last foraging bout:

(1) Proportion of visits to high-quality flowers: number of visits to high-quality flowers divided by the total number of visits,

(2) Proportion of high-concentration sucrose solution collected: number of high-quality flowers collected divided by the total number of flowers collected, and

(3) Proportion of low-concentration sucrose solution rejected: number of non-depleted low-quality flowers visited and not collected, divided by the total number of visits to low-quality flowers.

The first two principal components (PC1 and PC2) were retained, as they together explained 100% of the variance, capturing the combined influence of the three variables. We then combined PC1 and PC2 into a single "pickiness metric" by calculating their weighted sum based on the proportion of variance each component explained (see **Supplement S1** for full analysis).

Additionally, we applied K-Means clustering to classify bees into two distinct groups based on the combined influence of PC1 and PC2. The algorithm identified two clusters (**Fig. 2B**): (1) Low pickiness (N = 9 bees), representing bees with the lowest "pickiness metric" scores, and (2) High pickiness (N = 28 bees), representing bees with the highest scores.

(B) Estimation of absolute sucrose intakes

We inferred the absolute sucrose intakes of bees based on video analysis, using the number of high- and low-quality flowers collected per foraging bout and the theoretical sucrose content of 20% and 40% w/w sucrose solutions: (1) 20% w/w sucrose solution: with a density of 1.081 g/mL (Hofmann, 1977), a drop of 14 µL drop weighs approximately 15.134 mg, comprising 12.106 mg of water and 3.027 mg of sucrose, and (2) 40% w/w sucrose solution: with a density of 1.176 g/mL (Hofmann, 1977), a 14 µL drop weighs approximately 16.464 mg, comprising 9.882 mg of water and 6.588 mg of sucrose.

Results

The datasets from the main experiment and the complementary experiment (which replicated the main experiment with reversed flower colours; see **Supplement S2** for methodology and results) were combined for analysis. Naive bees in both experiments showed a tendency to visit yellow flowers first, with 60.9% (18/28 bees) and 67% (4/6 bees) making their very first visit to a yellow flower in the main and complementary experiments, respectively.

1. Bees in the High vs. Low flower array increased their foraging efficiency with experience

We first examined whether bees foraging on flower patches containing both high- and low-quality flowers favoured the high-concentration sucrose solution or collected solution from both flower types. Over successive foraging bouts, the bees significantly increased: (1) their proportion of visits to high-quality flowers, calculated as the number of visits to high-quality flowers divided by total visits (post-hoc Tukey test, bout 1 vs. bout 3: 50.5% ± 4.2% vs. 68.3% ± 4.2%, t-ratio = -6.20, $p < 0.0001$; N = 37 bees; **Fig. 2A**); (2) their proportion of high-concentration sucrose solution collected, calculated as the number of high-quality flowers collected divided by total flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 55.6% ± 4.6% vs. 87.7% ± 4.7%, t-ratio = -10.55, $p < 0.0001$; N = 37 bees; **Fig. 2A**), and (3) their proportion of low-concentration sucrose solution rejected, calculated as the number of non-depleted low-quality flowers visited and not collected, divided by total visits to low-quality flowers (post-hoc Tukey test, bout 1 vs. bout 3: 29.4% ± 7.0% vs. 74.0% ± 6.2%, t-ratio = -5.51, $p < 0.0001$; N = 37 bees; **Fig. 2A**).

(A) Bees in the High vs. Low flower array showed variability in pickiness

We observed high variability in the proportions of high-quality flower visits, high-concentration sucrose collection, and low-quality flower rejection (**Fig. 2A**), reflecting substantial interindividual differences in foraging behaviour. To capture these differences, we performed a Principal Component Analysis (PCA) on these three variables from the final foraging bout, when bees were expected to have developed stable foraging behaviour after three successive bouts. We then applied K-means clustering, identifying two distinct bee clusters (**Fig. 2B**): High pickiness (N = 28 bees) and Low pickiness (N = 9 bees).

After three foraging bouts, bees in the high pickiness cluster made significantly more visits to high-quality flowers than those in the low pickiness cluster (GLMM: $\chi^2 = 16.41$, df = 1, $p < 0.0001$; mean last bout = 75% ± 0.03 for High pickiness cluster vs. mean last bout = 51.78% ± 0.04 for Low pickiness cluster; **Fig. 2C**). High pickiness bees also collected a higher proportion of high-concentration sucrose solution (GLMM: $\chi^2 = 53.79$, df = 1, $p < 0.0001$; mean last bout = 97.82% ± 0.01 for High pickiness cluster vs. mean last bout = 57.33% ± 0.04 for Low pickiness cluster; **Fig. 2C**), and rejected a greater proportion of low-concentration sucrose solution (GLMM: $\chi^2 = 43.01$, df = 1, $p < 0.0001$; mean last bout = 98.13% ± 0.01 for High pickiness cluster vs. mean last bout = 36.63% ± 0.08 for Low pickiness cluster; **Fig. 2C**).

(B) The degree of pickiness was correlated with the quality of the first flowers visited

Bees in the High pickiness cluster were more likely to make their first-ever visit to a high-quality flower compared to those in the Low pickiness cluster (post-hoc Tukey test, High pickiness cluster vs. Low pickiness cluster: 60.1% ± 16.4% vs. 27.6% ± 19.4%; z = 1.48, p = 0.138, N = 37 visits; **Fig. 2D**). This effect became statistically significant when considering only the first two flower visits (post-hoc Tukey test, High pickiness cluster vs. Low pickiness cluster: 61% ± 8.13% vs. 28.2% ± 11.36%; z = 2.19, p = 0.028, N = 74 visits; **Fig. 2D**). This finding suggests that early exposure to high-quality flowers drive bees to become more selective, whereas initial visits to low-quality flowers may decrease selectivity in subsequent choices.

2. Bees across arrays and clusters improved foraging efficiency through variable foraging behaviour

Next, we examined the foraging behaviour of bees across bouts, comparing flower arrays (High vs. Low and High vs. Water) and clusters (High pickiness and Low pickiness). All groups significantly increased their estimated sucrose intake per unit of time with each successive bout (GLMM: $\chi^2 = 90.76$, df = 2, $p < 0.0001$, N = 52 bees). This improvement rate was consistent across groups at the same foraging stage (GLMM: $\chi^2 = 0.77$, df = 2, $p = 0.68$). We then analysed the foraging behaviour of each bee group in more detail:

(A) High pickiness bees

High pickiness bees maintained consistent foraging durations across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 3.96 min ± 0.53 vs. 3.41 min ± 0.45, z-ratio = 1.06, *p* = 0.54; **Fig. 3A**). They increased the number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 10.24 flowers ± 0.89 vs. 12.22 flowers ± 1.04, z-ratio = -2.73, *p* = 0.017; **Fig. 3B**) but did not significantly increase the proportion of high-concentration sucrose solution collected (post-hoc Tukey test, bout 1 vs. bout 3: 61.6% of high-quality flowers collected ± 3.59 vs. 97.6% ± 1.01, z-ratio = -1.81, *p* = 0.17; **Fig. 3C**).

The bees reduced revisits to previously depleted flowers (post-hoc Tukey test, bout 1 vs. bout 3: 7.44 revisits ± 1.74 vs. 4.62 revisits ± 1.15, z-ratio = 2.63, *p* = 0.02; **Fig. 3D**). Overall, bees from this cluster showed an increase in estimated sucrose intake across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 45.7 mg ± 4.66 vs. 61 mg ± 6.04, z-ratio = -4.47, *p* < 0.0001; **Fig. 3E**). In the final test, 92.6% of bees first visited the high-quality flower patch (**Fig. 3F**).

(B) Low pickiness bees

By contrast, Low pickiness bees increased their foraging duration over bouts (post-hoc Tukey test, bout 1 vs. bout 3: 6.80 min ± 0.52 vs. 4.14 min ± 0.31, z-ratio = 6.16, *p* < 0.0001; **Fig. 3A**). They decreased the number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 12.68 flowers ± 0.61 vs. 10.57 flowers ± 0.52, z-ratio = 5.11, *p* < 0.0001; **Fig. 3B**) while significantly shifting their collection of sucrose solution towards high-quality flowers (post-hoc Tukey test, bout 1 vs. bout 3: 39.1% of high-quality flowers collected ± 6.74 vs. 55.2% ± 6.57, z-ratio = -7.18, *p* < 0.0001; **Fig. 3C**).

The bees reduced flower revisits (post-hoc Tukey test, bout 1 vs. bout 3: 12.59 revisits ± 1.85 vs. 9.78 revisits ± 1.46, z-ratio = 3.26, *p* = 0.003; **Fig. 3D**), while their estimated sucrose intakes remained stable across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 65.2 mg ± 3.47 vs. 68.8 mg ± 3.65, z-ratio = -1.69, *p* = 0.21; **Fig. 3E**). In the final test, 55.6% of bees first visited the high-quality flower patch (**Fig. 3F**).

(C) High vs. Water flower array

In this flower array, where only high-concentration sucrose solution was available, bees nearly halved their foraging duration over successive bouts (post-hoc Tukey test, bout 1 vs. bout 3: 7.42 min ± 0.77 vs. 3.88 min ± 0.4, z-ratio = 5.96, *p* < 0.0001; **Fig. 3A**) while maintaining a steady number of flowers collected (post-hoc Tukey test, bout 1 vs. bout 3: 10.13 flowers ± 0.69 vs. 9.49 flowers ± 0.65, z-ratio = 1.25, *p* = 0.42; **Fig. 3B**).

Bees reduced flower revisits by nearly threefold (post-hoc Tukey test, bout 1 vs. bout 3: 24.04 revisits ± 3.99 vs. 8.8 revisits ± 1.57, z-ratio = -1.81, *p* < 0.0001; **Fig. 3D**), while their estimated sucrose intakes remained consistent across bouts (post-hoc Tukey test, bout 1 vs. bout 3: 66.9 mg ± 4.9 vs. 62.2 mg ± 4.59, z-ratio = 1.61, *p* = 0.24; **Fig. 3E**). In the final test, 86.7% of bees first visited the high-quality flower patch (**Fig. 3F**).

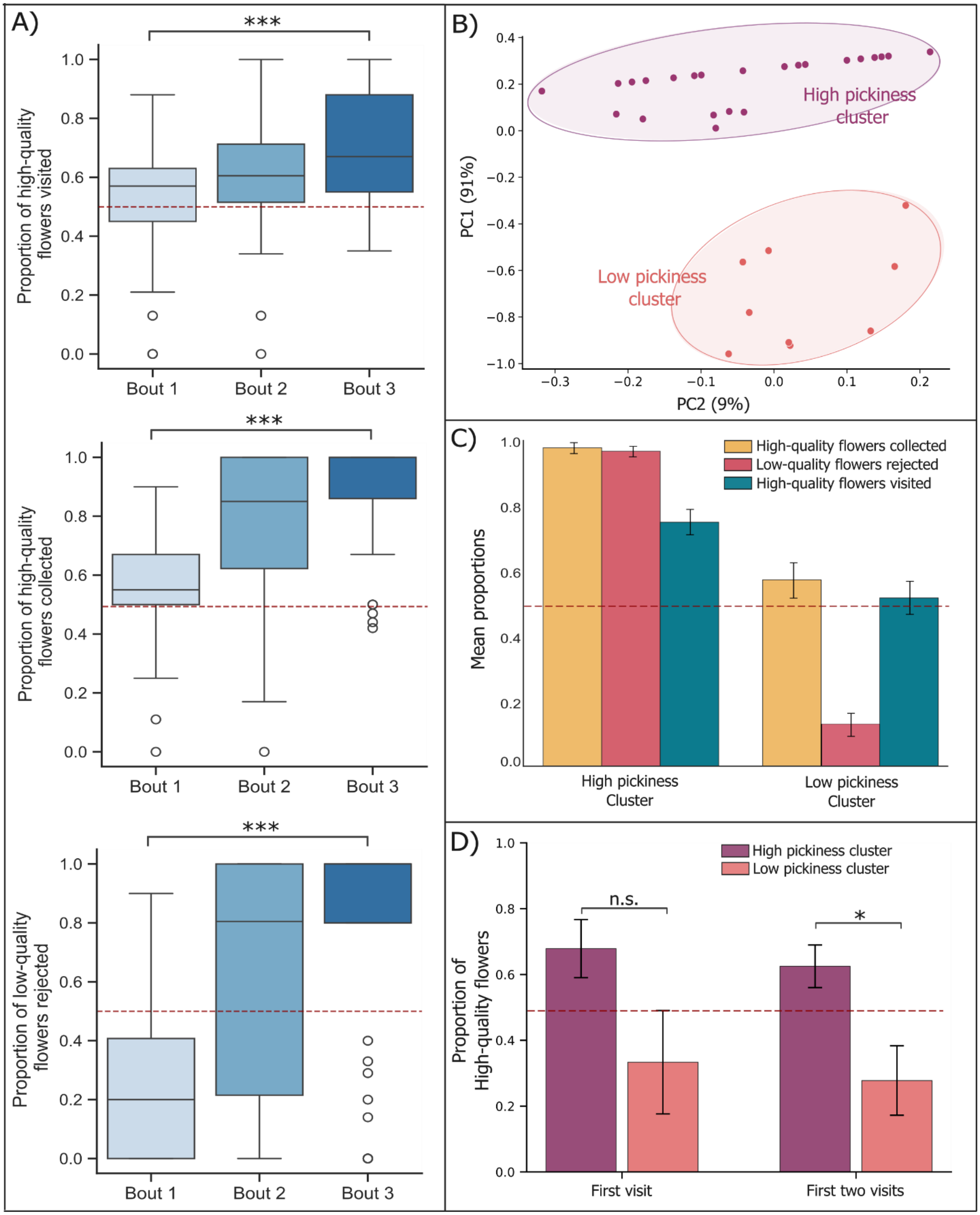
A)
***
Proportion of high-quality flowers visited
1.0
0.8
0.6
0.4
0.2
0.0
Bout 1
Bout 2
Bout 3
***
Proportion of high-quality flowers collected
1.0
0.8
0.6
0.4
0.2
0.0
Bout 1
Bout 2
Bout 3
***
Proportion of low-quality flowers rejected
1.0
0.8
0.6
0.4
0.2
0.0
Bout 1
Bout 2
Bout 3
B)
PC1 (91%)
0.4
0.2
0.0
−0.2
−0.4
−0.6
−0.8
−1.0
High pickiness cluster
Low pickiness cluster
−0.3
−0.2
−0.1
0.0
0.1
0.2
PC2 (9%)
C)
Mean proportions
1.0
0.8
0.6
0.4
0.2
0.0
High-quality flowers collected
Low-quality flowers rejected
High-quality flowers visited
High pickiness Cluster
Low pickiness Cluster
D)
Proportion of High-quality flowers
1.0
0.8
0.6
0.4
0.2
0.0
High pickiness cluster
Low pickiness cluster
n.s.
*
First visit
First two visits

Figure 2: Foraging efficiency in the High vs. Low flower array. A) Box plots of the proportions of bees: (1) visiting high-quality flowers, (2) collecting high-quality flowers, and (3) rejecting low-quality flowers across foraging bouts (N = 37 bees). Boxes represent the interquartile range (IQR), the inner line the median, and whiskers extend to the smallest and largest values within 1.5 times the IQR from the quartiles. Statistical significance is indicated as ******* ($p < 0.001$, post-hoc Tukey test); **B)** Scatter plots of bee clustering based on PCA of the three foraging pickiness variables (1), (2), and (3). The y-axis shows the first principal component (PC1), explaining 91% of the variance, and the x-axis shows the second principal component (PC2), explaining 9% of the variance. Each point represents a bee (N = 37), colour-coded by cluster: Low pickiness (N = 9) and High pickiness (N = 28), as determined by K-means clustering; **C)** Bar plots of the mean proportions of variables (1), (2), and (3) for each pickiness clusters; **D)** Bar plots of the proportions of high-quality flowers visited during the first flower visits for each bee cluster. Error bars represent standard errors of the means, and statistical significance is indicated as ***** ($p < 0.05$) and **n.s.** ($p > 0.05$, post-hoc Tukey tests).

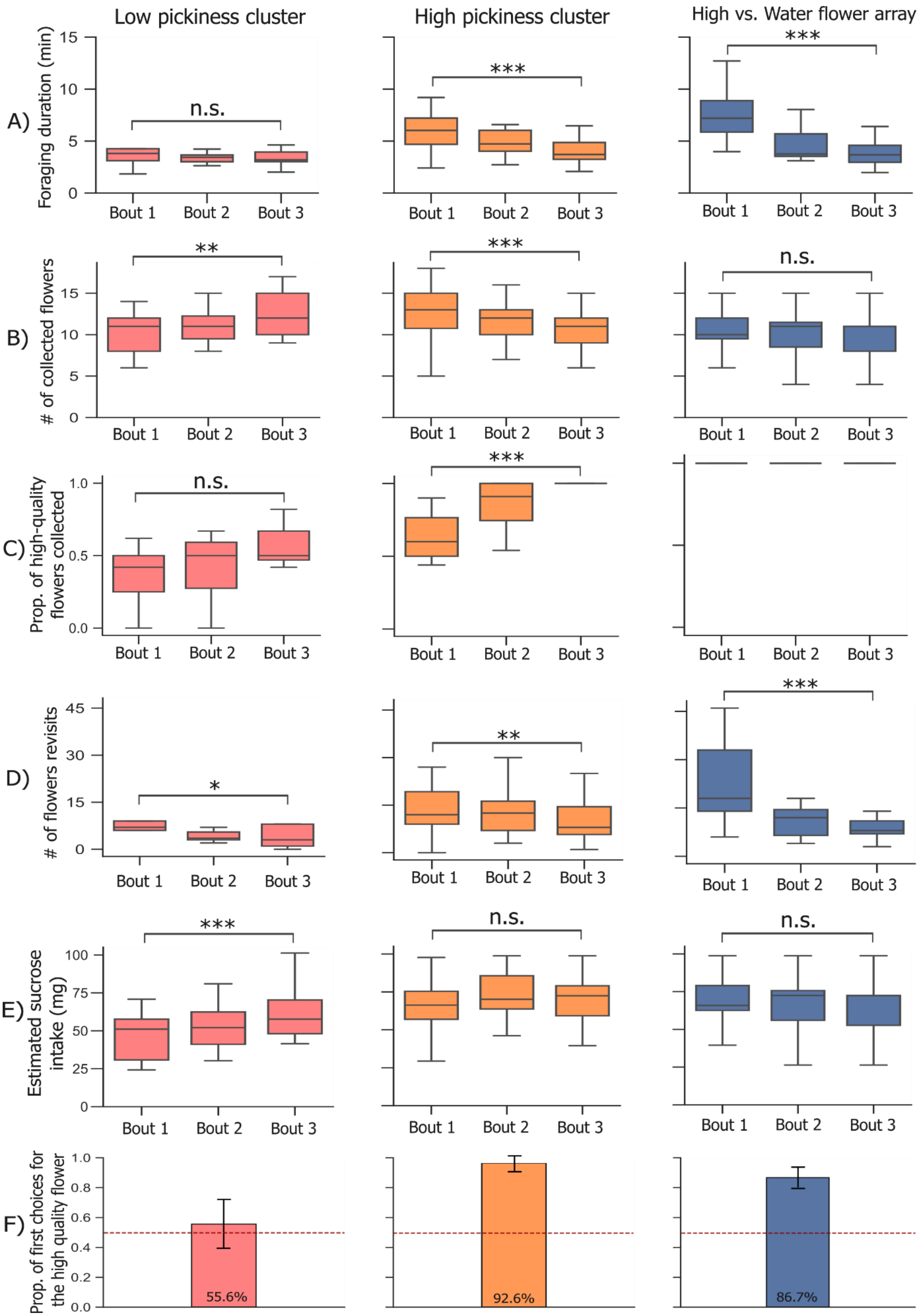
Low pickiness cluster
High pickiness cluster
High vs. Water flower array
A)
Foraging duration (min)
15
10
5
0
n.s.
***
***
Bout 1
Bout 2
Bout 3
B)
# of collected flowers
15
10
5
0
**
***
n.s.
C)
Prop. of high-quality flowers collected
1.0
0.5
0.0
n.s.
***
D)
# of flowers revisits
45
30
15
0
*
**
***
E)
Estimated sucrose intake (mg)
100
75
50
25
0
***
n.s.
n.s.
F)
Prop. of first choices for the high quality flower
1.0
0.8
0.6
0.4
0.2
0.0
55.6%
92.6%
86.7%

Figure 3: Foraging efficiency of bees across flower arrays. A) Foraging duration per bout (minutes); **B)** Number of flowers collected per bout; **C)** Proportion of high-concentration sucrose solution collected per bout; **D)** Number of flowers revisited per bout; **E)** Estimated sucrose intake per foraging bout (mg), and **F)** Proportion of first visit on the high-quality flower in the final test (N = 52 bees). Each boxplot shows the median (centre line), interquartile range (IQR, represented by the box), and whiskers extending to the smallest and largest values within 1.5 times the IQR from the quartiles. Error bars represent standard errors of the predicted probabilities. Statistical significance is indicated as ******* ($p < 0.001$), ****** ($p < 0.01$), ***** ($p < 0.05$), and **n.s.** ($p > 0.05$), based on post-hoc Tukey tests.

Discussion

This study investigated how the difference between good and poor flowers in mixed-quality patches influence bees' flower choices, addressing the gap in understanding interindividual variability in the foraging behaviour among bees. We showed that foragers rapidly improved foraging efficiency across successive bouts, achieving similar sucrose intake rates after three bouts, regardless of the flower array ("favourable", with high- and low-quality flowers, or "extreme", where only half the flowers were rewarding). This main finding supports our prediction and is to some degree in line with Optimal Foraging Theory (OFT) predictions, which suggests that nectarivores should maximise their net energy intake rate (Heinrich, 1979a; Waddington and Holden, 1979; Pyke and Starr, 2021). Additionally, we observed substantial variability in foraging behaviour, particularly in flower selectivity, with some bees showing a strong preference for high-quality flowers while others were less selective. This result is consistent with the high interindividual variability reported in bumblebees foraging in heterogeneous environments (Woodgate et al., 2016).

Bees in our study showed considerable variability in how they improved their foraging efficiency; High pickiness bees collected less sucrose solution over bouts but of higher concentration, thus prioritising quality over quantity. In contrast, bees from the low pickiness cluster increased the total volume of sucrose they collected, regardless of sucrose concentration. While bees from both clusters learned and improved with each bout, they still maintained distinct foraging behaviours across bouts. These findings align with those of Chittka et al. (2003), where individual bees demonstrated consistent speed-accuracy trade-offs, retaining their initial foraging behaviours even as they learned. Similar trade-offs have been observed in other studies, with bees balancing speed and accuracy (Burns and Dyer, 2008), or reward value and foraging effort (Lihoreau et al., 2011; Pattrick et al., 2023). Such variability in foraging behaviour may be advantageous in natural environments, given the spatial and temporal unpredictability of resources. Moreover, variability in individual foraging behaviour may enhance overall colony performance (Muller and Chittka, 2008; Holland et al., 2021). In line with this, Hagbery and Nieh (2012) observed that generalist bumblebees which do not specialise exclusively in nectar or pollen, could flexibly adapt their foraging behaviour in response to shifts in the colony workforce.

Interestingly, most bees did not increase their estimated absolute sucrose intake over successive bouts; only low pickiness bees showed an increase. Bees in this cluster had lower estimated intakes during the first two foraging bouts compared to high-pickiness bees and those foraging in the array with only one rewarding flower type. For high-pickiness bees, their focus on high-quality flowers likely constrained their ability to collect significantly more sucrose over bouts: in our setup, only half of the flowers in each patch were either highly rewarding or rewarding at all, increasing the likelihood of revisiting previously depleted flowers as the best rewards diminished. Previous studies have shown that bees do not visit all flowers in a patch (Goulson, 2000; Hemingway et al., 2024). According to the optimal departure rule, pollinators should leave a patch when their reward acquisition rate declines (Cresswell, 1990; Goulson, 2000). However, we found that naive bees, regardless of group, did not collect markedly fewer rewards during their first bout despite longer foraging durations and frequent revisits to depleted flowers. This suggests that bees did not return to the nest when sucrose acquisition rates decreased; otherwise, we would have observed lower estimated sucrose intakes on the first bout, due to reduced foraging efficiency. Instead, it is likely that inexperienced bees were exploring their new environment, similar to wild bumblebees making exploration flights during their initial foraging trips (Woodgate et al., 2016). Notably, high-pickiness bees collected over 15% fewer flowers in their final bout compared to their first, while maintaining constant total sucrose collection. This behaviour suggests that bees may aim for a fixed energetic target before returning to the nest, rather than a fixed collection volume or foraging duration. Furthermore, it indicates that bees are willing to return with partially empty crops (see Schmid-Hempel et al., 1985). However, explicit testing would be necessary to confirm such fixed energetic target hypothesis.

One result to further consider is that all bee groups in our study improved their foraging efficiency at a similar rate, achieving comparable estimated sucrose intakes by the same bout. This suggests that bees, to some extent, may be capable of compensating for less favourable initial conditions by adapting their foraging behaviour. This finding should nonetheless be considered with caution, as we did not directly measure the bees' actual sucrose intakes but rather inferred it through video analysis and calculations (see B. in the data analysis section). Notably, our results may underestimate the sucrose solution collected from low-quality flowers, as these were often probed for less than a second and thus considered non-collected in the analysis. However, Lechantre et al (2021) showed that bumblebees can imbibe up to 2 µL of solution per second, indicating that even brief probing may yield measurable rewards.

Our study also raises questions about the factors influencing differential foraging behaviours, such as flower-quality pickiness. In the favourable array containing both high- and low-quality flowers, the majority of bees became highly selective for high-quality flowers. The degree of pickiness was correlated with the bees' initial flower visits, which were predominantly on flowers with high-concentration sucrose solution.

A likely explanation for this variability in pickiness is flower constancy. Previous studies have shown that bees remain constant to flowers offering high rewards but explore alternative options when rewards are low (Chittka et al., 1999; Grüter and Ratnieks, 2011; Nityananda and Chittka, 2020). This mechanism may explain why bees in our study strongly favoured high-quality flowers when first exposed to them, whereas bees initially visiting low-quality flowers exhibited greater variability in subsequent choices. While flower constancy was long thought to result from cognitive limitations (Waser, 1986, 1986; Chittka et al., 1999), more recent studies suggest it may function as an adaptive strategy (Gegear and Thomson, 2004). Recent simulations have shown that highly flower-constant bee colonies exploited only 30–50% of available flower species, while indiscriminate foragers exploited nearly all species (Grüter et al., 2024).

Can pickiness be solely attributed to the quality of the first few flower visits? The relative strength of the correlation suggests that other factors may also be at play. For example, bees are known to have variable sensitivity thresholds for sucrose, which could drive individual differences in specialisation on rewards of varying quality (Page et al., 2006; Riveros and Gronenberg, 2010). Additionally, differences in learning ability among bumblebees (Raine et al., 2006) might explain why bees in the low pickiness cluster did not favour the high-quality patch in the final test. Although all bees in our study increased their visits to high-quality flowers over successive bouts, they did not do so at the same rate. Would every bee have eventually become highly selective in our setup? Shifting foraging behaviour can be energetically costly, especially in dynamic environments (DeWitt et al., 1998), like our changing flower array layouts in each bout. An interesting research direction would be to experiment with varying starting conditions to determine whether bees eventually converge on the same optimal foraging behaviour, and when this convergence happens, providing insights into the limits of foraging flexibility.

It is important to note that most high-concentration flowers were yellow in this experiment. Contrary to our expectation that blue flowers would attract bees first due to innate preferences (Gumbert, 2000; Raine and Chittka, 2007), over two-thirds of the first visits were made to yellow flowers. This unexpected preference may stem from yellow flowers reflecting more light across a broader range of wavelengths, resulting in higher overall brightness. Brightness is a key factor influencing bee preferences (Sletvold et al., 2016) and may explain this initial preference, even though the blue flowers in our setup had greater spectral purity and saliency in the white arena—traits typically associated with higher bee attraction (Lunau, 1990; Goulson, 2000).

While our findings suggest that bees aimed to optimise energy intake, it is important to note that not all energetic costs of foraging were fully accounted for, such as the cost of flight: in our setup, flowers within patches were positioned closely enough for bees to walk between them, allowing those who visited neighbouring flowers to potentially conserve energy. Additionally, the energy expenditure of individual bees likely varied depending on the weight of the sucrose loads carried by each bee (Wolf et al., 1989; Combes et al., 2020). While bees quickly learned in our simple flower arrays within a few consecutive bouts, natural environments are far more complex, with differences between rich and poor flowers being less distinct and predictable. Moreover, our small flight arena represented a "local" scale, as described by Sommer et al. (2022). In this controlled setting, bees likely encountered flower signals almost immediately (Heinrich, 2004), which is not typically the case in natural environments. Nonetheless, our findings highlight the rapid adaptability of foraging bumblebees within just three bouts and open interesting research avenues to explore how environmental conditions, initial experiences, and foraging behaviour interact. A deeper understanding of these mechanisms could provide valuable insights into the ecological success of bumblebees as pollinators across diverse and dynamic habitats.

Supplementary Material

S1 presents the statistical analysis of the main experiment, while **S2** provides the statistical analysis of the complementary experiment. **S3** includes the reflectance curves of the artificial flowers, and **S4** the layout patterns of the flower arrays. **S5** features video examples of bees foraging during the experiment. **S6** and **S7** contain the datasets for the main and complementary experiments, respectively. All statistical analyses and datasets are publicly available on Zenodo (https://doi.org/10.5281/zenodo.14524634).

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Chapter 2 – Bumblebees do not prefer consistent floral scents over variable ones

Mélissa Armand[1], Lisa Zeilmann[1], Christian Weinzettl[1] and Tomer J. Czaczkes[1]

[1]Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

Abstract

To attract pollinators, flowering plants evolve diverse sensory traits into compelling signals. Floral scent, in particular, plays a key role in drawing bees from a distance and shaping their foraging choices. Scent composition varies widely, including across flowers of the same plant species. Yet, it is unclear whether scent variability influences bee flower choices, and thus whether plants would be under selection to minimise variation in their scent composition. Since bees typically avoid variability in rewards, we hypothesised they would favour flowers with more consistent scents. To test this, we trained individual bumblebees (*Bombus terrestris*) on two equally rewarding flower arrays: one with a consistent scent blend across flowers, and the other with variable scent blends between flowers. Contrary to expectations, bees showed no preference for scent consistency. They readily foraged from both arrays across bouts and did not favour either flower type in the binary choice test. To the best of our knowledge, this is the first study to examine how bees respond to scent variability. A better understanding of scent profile preferences in pollinators could offer new insights into their co-evolution with plants and the development of floral traits. More broadly, further research is needed on how pollinators respond to variability and unpredictability in neutral cues like scent or colour, a largely overlooked aspect of foraging decision-making.

Introduction

Most flowering plants depend on pollinators for reproduction (Klein et al., 2007), so their flowers act like billboards, using various colours, shapes, and scents to attract them (Dobson, 1994). Floral scents, especially, play a key role in pollination (Burkle et al., 2020): scent bouquets attract bees from far away (Raguso, 2004) and often serve as bees' primary cue for deciding whether to land on a flower (Kunze et al., 2001; Raguso, 2008a; Sprayberry, 2018). Yet, despite their influence on bees' foraging decisions (Farré-Armengol et al., 2015; Larue et al., 2016), the role of scent in flower choices remain understudied in comparison to flower colours and shapes (Fenster et al., 2004; Raguso, 2008b).

Floral scents consist of complex blends of volatile organic compounds (Knudsen et al., 2006), released from various parts of the flower (Pichersky et al., 1994; Raguso and Pichersky, 1999). These scent bouquets act as unique floral identifiers (Raguso, 2008a) and are highly diverse across plant species (Raguso and Pichersky, 1999; Levin et al., 2003). Scent composition can also vary across plant populations and even among individual flowers within the same species (Raguso et al., 2003; Burdon et al., 2015; Delle-Vedove et al., 2017). However, the causes of intraspecific scent variation remain poorly studied and understood (Majetic et al., 2009; Raguso, 2020), as well as its effects on pollinator foraging behaviour.

Scent cues allow flower-visiting insects to associate flowers with pollen and nectar rewards (Kevan and Baker, 1983; Wells and Wells, 1985; Giurfa, 2007), and help them distinguish between plant species (Dobson, 1994). Both honeybees and bumblebees can detect differences in floral scent blends (Laloi and Pham-Delègue, 2004; Wright et al., 2005), and small variations in compound ratios were shown to strongly affect their flower choices (Dobson, 1994; Raguso, 2004; Tan and Nishida, 2012; Solís-Montero et al., 2018). Like floral colours, bees have innate preferences for certain floral volatiles or scent blends (Raguso, 2008a; Schiestl and Dötterl, 2012). However, it is unclear whether bees also prefer certain patterns of scent variability.

Floral scent is a highly variable trait that plants can adjust to reflect their current state (Dudareva et al., 1996; Dobson, 1994). For instance, scented nectar can inform pollinators about reward availability (Heinrich, 1979; Raguso, 2004; Gervasi and Schiestl, 2017). Plants can also modify their scents to better attract pollinators (Dudareva et al., 2004; Raguso, 2008a; Leonard et al., 2011). For example, some flowers adjust the intensity of their scent emissions throughout the day to match pollinator activity (Loughrin et al., 1990; Raguso, 2008b; Wright and Thomson, 2005). Scent composition may also vary at different stages of flower development (Majetic et al., 2015; Burkle et al., 2020). Do bees favour plant species with more consistent or variable scent profiles across flowers?

Pollinators not only respond to floral traits but also influence how these traits evolve through selection pressure, including scent (Parachnowitsch et al., 2013; Schiestl and Johnson, 2013; Ollerton et al., 2011). Stabilising selection driven by pollinator preferences is well-established for flower colour (Goulson, 1999; Whibley et al., 2006), and similar selection may also shape scent composition (Huber et al., 2005; Mant et al., 2005; Salzmann et al., 2007). The pollination syndrome hypothesis suggests that unrelated plant species visited by similar pollinators tend to develop similar floral traits, such as scent composition (Fenster et al., 2004; Dobson, 2006; Farré-Armengol et al., 2020), although this idea remains debated (Rosas-Guerrero et al., 2014; Ollerton et al., 2015).

Bumblebees tend to specialise and forage on a few flower species (Heinrich, 1979; Chittka et al., 1999). Such flower constancy benefits plants by ensuring that bees repeatedly visit the same species, increasing pollination efficiency (Heinrich, 1977; Waser, 1986). Like colours, scents promote flower constancy in pollinators (Gegear and Laverty, 2005; Gegear, 2005). In turn, this flower constancy probably contributes to stabilising floral traits, including scent profiles (Chittka et al., 1999; Goulson, 1999). This tendency to be flower constant may reflect a broader preference for consistency in bee foraging decisions. In fact, bees typically exhibit an aversion to variability and unpredictability in rewards (see review by Anselme, 2018). Similarly, we propose that bees may favour plant species with more consistent scent profiles across flowers, potentially placing selection pressure on plants to tightly control their scent composition.

Here, we investigated whether bumblebees (*Bombus terrestris*) prefer flowers with either consistent or variable scents. To test this, we trained individual bees on two equally rewarding arrays of artificial flowers: all yellow or all green. In one array, all flowers contained sucrose solution scented with a fixed ratio of two artificial food flavourings, creating a consistent scent bouquet. In the other array, flowers had varying ratios of a different pair of scents, making varying, unpredictable scent bouquets. We hypothesized that bees would favour the consistent scent flower, being more predictable than the other flower. We predicted that in a binary choice test, bees would first visit the flower colour associated with the consistent scent.

Material and Methods

Colony setup

Commercial *Bombus terrestris* colonies were purchased from Koppert (The Netherlands) and kept under controlled laboratory conditions at 22–24°C with a 14:10 light:dark cycle. Colonies were housed in wooden nestboxes, each connected to its respective flight arena (60 × 50 × 35 cm) leading to a small chamber (6 × 5 × 3 cm). The chamber featured a second tube that provided direct access to the arena and was fitted with transparent, removable shutters to regulate bee movement between the nest and arena (see apparatus **Fig. 1**).

Bees were provided daily with pollen balls made from a mix of organic flower pollen pellets and 35% (w/w) sucrose solution, placed directly in the nestboxes. During the day, workers foraged freely on artificial flowers in the flight arena, which offered 35% (w/w) sucrose solution and were regularly refilled. Active foragers were captured and marked on the thorax with uniquely numbered, coloured tags, and considered for selection in the experiment on the same day. A total of 48 bees participated in the experiment from five colonies in May–June 2022 (see colony details in **Supplement S1**).

Artificial flowers

Each artificial flower consisted of a transparent plastic cup with a white lid (height: 4.5 cm, diameter: 3.8 cm), topped with a 2 mm-thick disc of coloured rubber foam. At the centre, a small opaque white resin cup (diameter: 4 mm, depth: 6 mm) was inserted into a pre-cut hole and filled with sucrose solution (**Fig. 1**).

In the experiment, flowers were either yellow (peak reflectance: ~540–700 nm) or green (peak reflectance: ~530 nm; see **Supplement S2** for reflectance curves). We selected these colours for their perceptual similarity while still allowing bees to differentiate them (see control experiment below), and to avoid strong innate preferences typically observed for blue or violet flowers (Gumbert, 2000; Raine and Chittka, 2007). Between experimental sessions, bees were pre-trained on bicoloured, half green half yellow flowers, to ensure they associated sucrose rewards equally with both flower colors used in the experiment (Raine and Chittka, 2008).

During training, bees foraged on an array of flowers consisting of a 3 × 3 grid of either all-yellow or all-green flowers. In the binary choice test, the array contained 5 green and 5 yellow flowers, arranged in two front rows of three flowers and a third row of four flowers (see **Fig. 1** below). Flowers were spaced 3.5 cm apart and mounted on a grey-painted plate matching the all-grey arena. The plate ensured consistent flower placement and allowed for easy flower replacement between foraging bouts.

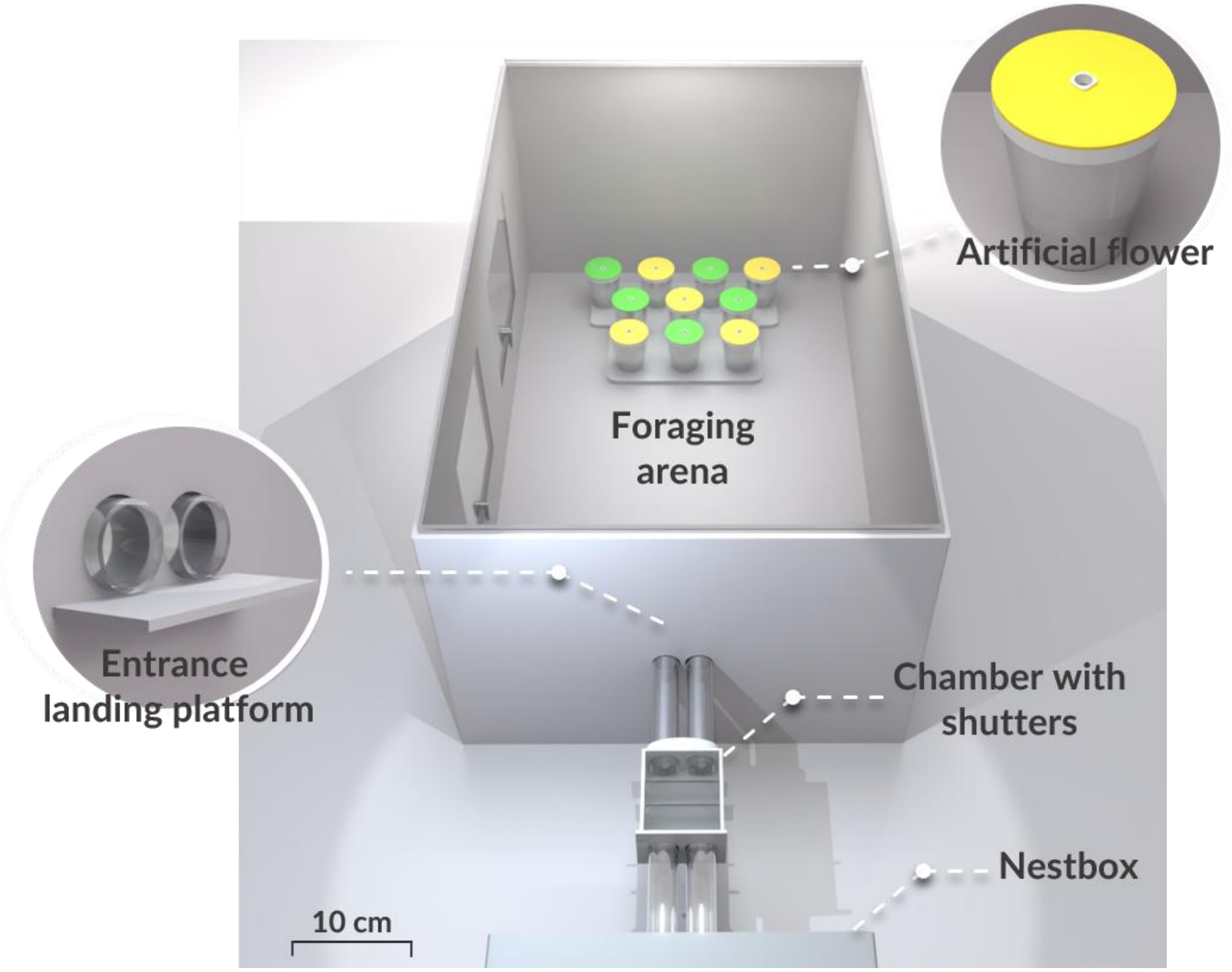

Figure 1: Top view of the experimental setup, to scale. The 3D model, created in Blender, illustrates a binary choice bout with a mixed flower array of yellow and green flowers, arranged in a "yellow biased" layout (*i.e.*: two yellow flowers on the front row).

Scented sucrose solutions

Artificial flowers provided 35% w/w sucrose solution at a fixed volume, determined individually for each bee based on an estimate of its honey crop size (see below). Sucrose solutions were scented using strawberry, rose, lemon, or vanilla food flavourings (Seeger, Springe, Germany). We created six artificial scent bouquets by mixing the flavourings in different combinations: strawberry–rose, lemon–vanilla, strawberry–vanilla, lemon–rose, strawberry–lemon, and vanilla–rose. Each combination was prepared in three different ratios: 1:1 (equal parts of both scents), 1:3 (25% scent A, 75% scent B), or 3:1 (75% scent A, 25% scent B).

Bees were familiarised with each scent (strawberry, rose, lemon and vanilla) 48 hours before the experiment, by placing filter papers soaked with 25 µL of each food flavouring in the four corners of the nestboxes, allowing airborne scents to disperse. This ensured that bees were not reluctant to collect sucrose solution during the experiment due to unfamiliar scents.

Estimation of crop size

To determine the appropriate volume of sucrose solution used per flower in the experiment, we first estimated the crop capacity of individual bees. Bee foraged on a 3 × 3 array of bicoloured flowers (half green, half yellow), with each flower providing 15 µL of a 35% w/w sucrose solution. We recorded the number of flowers collected over two consecutive foraging bouts and estimated the crop size of the bees by averaging the total volume collected across both bouts. This average volume was then divided by nine, and the resulting volume was used as the reward per flower during the experiment. This ensured that the bees could collect all available rewards in each foraging bout.

Training

After its crop size was estimated, each bee was trained for six consecutive foraging bouts on two different 3 × 3 flower arrays, alternating between them in each bout. Each flower array was associated with a flower colour (green or yellow) and a scent combination (strawberry–rose, lemon–vanilla, strawberry–vanilla, lemon–rose, strawberry–lemon, or vanilla–rose).

Bees experienced a distinct scent combination for each flower colour; for example, if one array had green flowers scented with strawberry–lemon, the other had yellow flowers scented with the remaining two scents (e.g. rose–vanilla). We assigned different scent combinations to each flower colour to ensure clear differentiation between flower types and allowed the use of three different scent ratios (1:1, 1:3, and 3:1) in the variable flower type, while maintaining a consistent 1:1 ratio in the consistent flower (see below).

The flower arrays were one of two types:

1. **Consistent flower array**: All flowers in the array had the same scent combination at a fixed 1:1 ratio (equal parts of both scents);
2. **Variable flower array**: Flowers in the array had varying scent ratios: some 1:1, some 1:3 (25% scent A, 75% scent B), and some 3:1 (75% scent A, 25% scent B).

For example, if a bee experienced green flowers as the consistent array, all green flowers would have strawberry–lemon in a fixed 1:1 ratio, and the yellow flowers in the variable array would contain rose–vanilla with varying scent ratios (1:1, 1:3, and 3:1).

Half of the bees experienced the consistent flower array as green and the variable array as yellow (n = 24 bees), and the other half the reverse (n = 24 bees). Bees were required to consistently collect sucrose solution from both array types to ensure they perceived each scent combination as an acceptable reward. Flowers were replaced with clean ones each new bout to prevent scent marks from influencing subsequent foraging (Goulson et al., 2000; Saleh et al., 2007).

Binary choice test

After the six training bouts, each bee was presented with an array of 10 flowers—5 yellow and 5 green, arranged so that neighbouring flowers alternated in colour. The flowers were unrewarded and filled with unscented plain water. Bees were randomly assigned one of two array layouts, where the front row contained either two green flowers and one yellow (“green-biased” layout), or the reverse (“yellow-biased” layout). We recorded the first flower choices as an indicator of preference.

Control experiment

A pilot was conducted before the main experiment to test whether bees could differentiate between green and yellow flowers. The setup mirrored the main experiment, where individual bees completed six training bouts to a 3 × 3 flower array of a single colour and alternating between arrays each bout, followed by a binary choice test with both flower colours.

Instead of being scented, one flower type offered 25 µL of a low-quality sucrose solution (15% w/w), while the other provided 35% w/w sucrose solution. This clear difference in reward quality allowed us to assess whether bees could correctly identify the flower colour associated with the higher-quality reward. All tested bees (n = 10) successfully chose first the flower colour associated with high-quality reward in the final test.

Data analysis

The binary choice test was video-recorded for each bee with a camera (Sony HDR-CX220) positioned above the flight arena. Bee behaviour was analysed using the event-logging software BORIS (v8.6). We tested the hypothesis that bees would favour the flower colour (green or yellow) associated with a consistent scent. To assess this, we recorded (1) the first flower visit and (2) the first 10 flower visits during the binary choice test, as indicators of preference.

(1) For the first flower visit, we built a generalized linear mixed model (GLMM) with a binomial distribution, using first flower scent choice (1 for consistent, 0 for variable) as the response variable and flower colour (green or yellow) as the predictor. Random effects included bee colony, first flower scent encountered (i.e., whether the first training bout involved the consistent or variable array), first flower colour encountered (green or yellow in the first training bout), and binary test layout ("green-biased" or "yellow-biased"). Predicted probabilities of first choice were assessed through post hoc pairwise comparisons with a Tukey correction.

(2) For the first ten flower visits, we fitted a GLMM with a binomial distribution, using flower scent choices (1 for consistent, 0 for variable) as the response variable and flower colour (green or yellow) as the predictor. Random effects included individual bee identities nested within their colony, first flower scent encountered, first flower colour encountered and binary test layout. Predicted probabilities of flower choices were evaluated through post hoc pairwise comparisons with a Tukey correction.

Data processing was conducted in Python (v3.11, Python Software Foundation, 2023) using the *pandas* library (McKinney, 2010) for data structuring and *seaborn* (Waskom, 2021) and *Matplotlib* (Hunter, 2007) for data visualization. Statistical analyses were performed in R (v4.1, R Core Team, 2022) using the *glmmTMB* package (Brooks et al., 2017) for GLMMs, and *emmeans* (Lenth, 2020) for post hoc tests. Model residuals were evaluated with the *DHARMa* package (Hartig, 2020). Complete statistical analyses and datasets are available on Zenodo (https://doi.org/10.5281/zenodo.14993082).

Results

First flower choice

31 of the 48 tested bees (64.6% ± 8.6%) first visited a yellow flower in the binary choice test, while 17 bees (35.4% ± 11.6%) chose a green flower. This difference was borderline significant (p = 0.059, two-tailed exact binomial test, 95% CI: 49.5–77.8%). Regarding flower scent choice, 27 bees (56.3% ± 9.5%) chose a flower associated with variable scents, and 21 bees (43.7% ± 10.8%) a flower associated with a consistent scent.

We then tested the combined effects of flower scent, colour, and random effects on bees' first flower choice (see model (1) in Data analysis). Bees showed no preference between flowers associated with consistent or variable scents (GLMM, binomial family; intercept: Estimate = -0.36 ± 0.50, z = -0.72, *p* = 0.47; N = 48; **Fig. 2A**), and flower colour had no significant effect on this choice ($X^2 = 0.073$, df = 1, *p* = 0.79).

First 10 flower visits

During their first ten visits in the binary choice test, bees visited yellow flowers 51.2% (± 3.3%) of the time and green flowers 48.8% (± 3.4%). Regarding flower scent choice, 50.3% (± 3.3%) of visits were to flowers associated with variable scents, and 49.7% (± 3.3%) to flowers associated with a consistent scent.

The GLMM (see model (2) in Data Analysis) revealed no preference between flowers associated with consistent or variable scents (binomial family; intercept: Estimate = -0.007 ± 0.14, z = -0.05, *p* = 0.96; N = 457; **Fig. 2B**), and flower colour had no effect on first 10 visits ($\chi^2 = 0.004$, df = 1, *p* = 0.95).

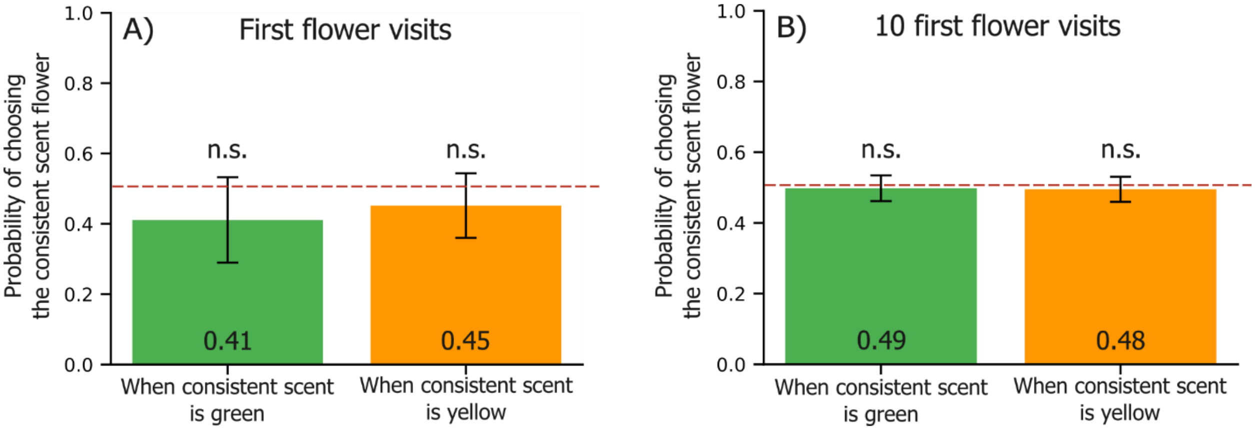

Figure 2: Estimated probabilities of choosing the consistent scent flower for each flower colour in the binary choice test. A) Proportion of choices in the first flower visit (N = 48 visits); **B)** Proportion of choices across the first 10 flower visits (N = 457 visits). Probabilities were derived from the GLMM and calculated through post hoc pairwise comparisons. The dotted red line represents a 50% chance of choosing either flower type. Error bars represent the standard errors of the predictions, and statistical differences within treatments are indicated as **n.s.** (*p* > 0.05).

Scents preferences

Overall, bees showed no preference for any scent bouquet in the binary choice test (Chi-square goodness-of-fit test: $X^2 = 1.75$, df = 5, *p* = 0.88; **Fig. 3A**) and did not favour any individual scent—lemon, rose, vanilla, or strawberry ($X^2 = 1.08$, df = 3, *p* = 0.78; **Fig. 3B**).

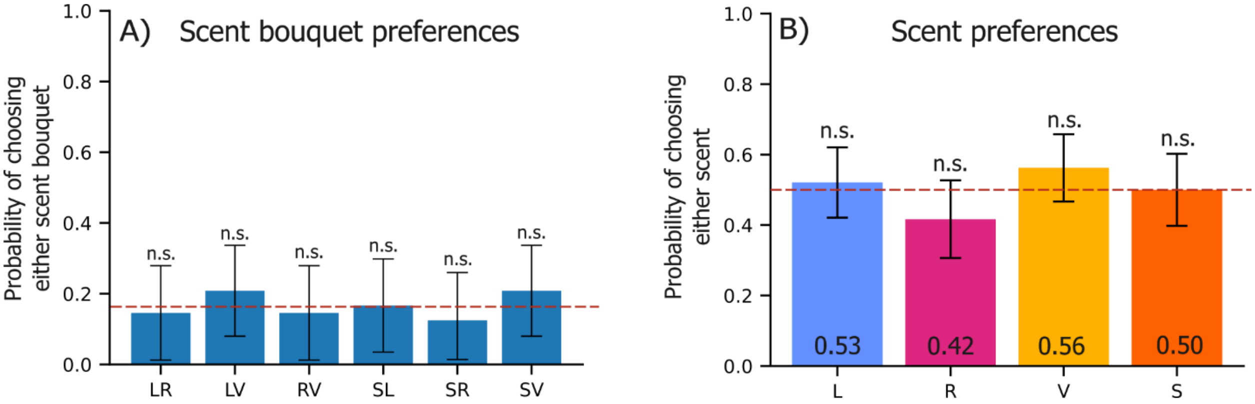

Figure 3: Probabilities of choosing each flower scent in the binary choice test. **(A)** Proportion of choices for each scent bouquet (N = 48 visits): lemon–rose (LR), lemon–vanilla (LV), rose–vanilla (RV), strawberry–lemon (SL), strawberry–rose (SR), or strawberry–vanilla (SV). The dotted line represents the expected random choice (16.67%). **(B)** Proportion of choices for each individual scent (N = 48 visits): Lemon (L), Rose (R), Vanilla (V), or Strawberry (S), with the dotted red line indicating a 50% chance of choosing either scent. Error bars represent standard errors, and statistical differences between scents are indicated as **n.s.** ($p > 0.05$).

Discussion

We tested whether bees had a preference between two equally rewarding flower arrays, yellow or green, one with consistent scents across flowers and the other with variables scents between flowers. Contrary to expectations, bees showed no preference for flowers with a consistent scent. During training, they readily collected sucrose solution flavoured with varying scent combinations and ratios, and in the binary choice test, they did not favour the flower colour associated with a consistent scent. To our knowledge, this is the first study to explicitly test whether bees prefer consistent or variable scents—or any other neutral cue like colour or shape—independently of reward variation.

Every tested bee collected all sucrose rewards in both flower arrays, regardless of scent composition. This reflects bees' ability to rapidly associate scents with rewards (Kunze and Gumbert, 2001; Wright and Schiestl, 2009; Giurfa, 2007), even when they have innate preferences for specific scent volatiles (Milet-Pinheiro et al., 2013; Raguso, 2008a). Surprisingly, bees visited and accepted every flower in the variable array, despite previous findings that bumblebees exhibit even stronger flower constancy when flowers differ in multiple sensory cues, such as scents and colours (Wells and Wells, 1985; Gegear and Laverty, 2001; Gegear, 2005). However, recent research has challenged the idea of high flower constancy in bumblebees; Yourstone et al. (2023) found that bees were less flower constant than expected, with only 23% of their foraging trips occurring on the same flower species.

In the binary choice test, bees showed a slight tendency to visit yellow flowers first, though this preference was not significant. Bees are known to have an innate preference for yellow flowers (Lunau, 1990; Gumbert, 2000). To ensure that choices were based on learned associations, we used unscented, unrewarded flowers in the binary test. Hence it is unclear whether scent preferences would have outweighed colour preferences if both cues were present simultaneously. Notably, Larue et al. (2015) found that floral scent had a stronger influence than visual traits in attracting flower-visiting insects.

Were bees in our experiment able to distinguish between scent combinations, particularly the different scent blend ratios in the variable flower array? Studies show that bees can detect individual volatiles within complex scent blends, influencing their flower choices (Laloi and Pham-Delègue, 2004; Locatelli et al., 2016), and honeybees can even perceive subtle differences in the ratio of two scents (Wright et al., 2005; Bateson et al., 2011). Moreover, since our flowers contained scented sucrose solution, bees could also taste them; Robertson (2019) suggests that olfactory and gustatory receptors may overlap in bumblebees. In nature, scented nectar contains volatile organic compounds, which pollinators use to assess reward availability before landing on a flower (Heinrich, 1979; Raguso, 2008b), and can impact their foraging behaviour (Raguso, 2004). Given this, it seems likely that bees could sense the variability in the variable flowers, and distinguish this from the fixed-ratio flowers.

Although no study has directly tested bees' preference for consistency in neutral cues, some have examined their responses to inconsistent rewarding cues. Honeybees tended to avoid choices where uncertain visual cues predict reward or punishment (Perry and Barron, 2013). Andrew et al. (2014) found that honeybees trained to discriminate between a rewarding and a punishing scent blend preferred a novel scent that was more distinct from the punishing one, rather than similar to the reward. Likewise, Lynn et al. (2005) showed that bumblebees favoured novel colours that minimised the risk of choosing an unrewarding flower. This phenomenon, known as "peak shift" (Hanson, 1959), occurs when animals develop a preference for a more extreme version of a rewarded stimulus to avoid similar, non-rewarded ones. These findings suggest that bees may prefer consistent cues over variable ones, to reduce uncertainty. Stress may further amplify this avoidance of inconsistent cues: Bateson et al. (2011) found that shaken honeybees were less likely to respond to ambiguous scents associated with rewards.

When it comes to rewards preferences, bees are generally risk-averse and tend to avoid variability (see review by Anselme, 2018). They typically prefer consistent nectar amounts over variable ones (Real, 1981; Waddington et al., 1981; Shafir et al., 1999), which is likely in part due to the psychophysics of reward perception (Kacelnik and Bateson, 1996). When resources are variable, bumblebees also forage less efficiently (Dunlap et al., 2017) and rely more on social information for flower choice (Smolla et al., 2016). However, their sensitivity to variability depends on context. In some contexts, bees showed indifference to fluctuations in nectar concentration or volume (Waddington, 1995; Fülöp and Menzel, 2000) and when variable distribution did not include null rewards (Drezner-Levy and Shafir, 2007). They may even favour variable rewards when advantageous: For example, bumblebees initially preferred consistent rewards but shifted to variable ones when colony nectar reserves were low, both in natural foraging conditions (Cartar, 1991) and in laboratory settings (Cartar and Dill, 1990).

Bees' preferences for specific floral volatiles are well documented (Knudsen et al., 2006; Farré-Armengol et al., 2017; Benelli et al., 2017; Bisrat and Jung, 2022), and they readily associate these scents with rewards (Wells and Wells, 1985; Wright and Schiestl, 2009; Giurfa, 2007). Bees can even retain scent memories longer than visual cues (Menzel, 1993; Kunze and Gumbert, 2001). Bumblebees, in particular, use floral scents as social cues, with foragers transferring scent compounds within the nest to inform nestmates (Molet et al., 2009). They also favour flowers that match the scents collected by successful foragers (Dornhaus and Chittka, 1999).

However, bees learn consistent scents more effectively than variable ones (Wright and Thomson, 2005; Wright and Schiestl., 2009). For instance, Wright et al. (2008) found that honeybees reject scent-modified flowers even if they contain familiar scent compounds, highlighting the importance of scent consistency for pollinator recognition. Many rewardless flowers emit weak or highly variable scent, likely to avoid detection by scent-learning pollinators (Jersáková and Johnson, 2006; Salzmann et al., 2007). Salzmann et al. (2007) found that rewarding orchids produce strong, consistent scents that bees can detect, whereas deceptive orchids emit weak, highly variable scents. Similarly, floral compounds that attract pollinators tend to be more consistent across populations and species, while non-attractive compounds show greater variability (Mant et al., 2005; Huber et al., 2005).

Nonetheless, floral scent remains a highly variable trait (Dudareva et al., 1996), even among individual flowers within the same species (Burdon et al., 2015). While plants adjust scent emissions to attract pollinators (Majetic et al., 2015; Burkle et al., 2020), scent bouquets are also influenced by environmental factors (Dudareva et al., 1999; Raguso, 2008b). Studies suggest that intraspecific variation in floral scent may help attract local pollinators (Soler et al., 2011; Larue et al., 2016; Vega-Polanco et al., 2023). Fülöp and Menzel (2000) propose that bees’ tolerance for scent variability may be an adaptation to cope with unreliable floral resources.

Floral scents, including scented nectar, likely serve as honest signals to pollinators (Gervasi and Schiestl, 2017; Burdon et al.,2020), Bees often select flowers based on their scent composition (Pichersky and Raguso, 2018; Knudsen and Gershenzon, 2020) or the intensity of scent emissions (Majetic et al., 2009; Parachnowitsch et al., 2013), which inform foragers about nectar and pollen availability. We suggest that bees are likely to respond to olfactory cues regardless of whether they are more variable or consistent, as long as they can reliably associate them with rewards.

Our findings highlight bees' ability to rapidly learn scent-reward associations and show that they forage equally on flower arrays with both variable and consistent scents, and show no preference between them.

This in turn suggests that plants may not be under strong selection to reduce inter-flower scent variability, at least in terms compound ratios. Maintaining tight control over a trait in the face of environmental variation is costly, and if no selection for this maintenance is present, we would expect such traits to fluctuate, as indeed is the case with intraspecific scent variation between flowers (Burdon et al., 2015; Delle-Vedove et al., 2017).

However, our controlled experiment likely oversimplified the complex sensory landscape bees navigate in nature, and further research is needed to understand how they respond to scent variability within flower patches. Despite its importance, the role of floral scent in bee foraging has been largely overlooked (Fenster et al., 2004; Raguso, 2004, 2008). More generally, future studies should examine whether bees' aversion to variability in rewards extends to other neutral cues like morphology or colour, as the foraging preferences of plant pollinators play a key role in shaping floral trait evolution (Ollerton et al., 2011).

Supplementary Material

S1 contains the dataset of the main experiment, **S2** provides the reflectance curves of the artificial flowers, and **S3** the statistical analysis of the experiment. All supplementary materials are available on Zenodo (https://doi.org/10.5281/zenodo.14993082).

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Chapter 3 – Testing the peak-end rule in bumblebees: lack of preference for a higher-reward sequence when the final reward is disappointing

Mélissa Armand[1], Pauline Riemer[1], Sophia Hagn[1], Jana Schweiger[1] and Tomer J. Czaczkes[1]

[1]Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

Abstract

The peak-end rule describes the tendency to evaluate experiences by their most intense and final moments, rather than considering the entire experience as a whole. While this cognitive bias is well-established in humans, studies on nonhuman animals are very limited. Bumblebees make foraging decisions largely based on past experiences, but whether peak-end effects influence their subsequent flower choices is still unknown. Here, we trained individual *Bombus terrestris* workers on two artificial flower types, alternating blue and yellow, over 12 consecutive foraging bouts. One flower type offered a sequence of three high-quality rewards (25 µL drops of 50% w/w sucrose solution: "consistent" sequence), while the other provided the same sequence but ended with an additional, lower-quality reward (25 µL drop of 20% w/w sucrose solution: "poor end" sequence). We then tested the bees' flower type preference in a final binary choice. Bees showed a strong preference for blue flowers, both in their initial and overall visits. Across all visits during a 1-minute period, they also favoured flowers associated with the "consistent" sequence, though this preference was significant only when these flowers were yellow. Interestingly, despite offering more sucrose per foraging bout, bees did not favour the "poor end" sequence flower. This study is, to our knowledge, the first to investigate peak-end effects in an insect. How bees evaluate sequential rewards when foraging remains largely unexplored, yet could provide valuable insights into nectar distribution and plant-pollinator co-evolution.

Introduction

Animals encounter countless options to choose from throughout their life, for example when selecting a nest, partner, or food sources when foraging. Such resources are typically encountered sequentially, requiring individuals to recall and evaluate each option when making decisions. Since memory is a costly and limited resource, individuals may base their judgements on key moments from past experiences rather than the entire experience. Fredrickson and Kahneman (1993) showed that people often rely on the most intense moment (the peak) and the final moment (the end) of an event—a phenomenon known as the peak-end rule. This heuristic is well-established and robustly supported by extensive human studies (see meta-analysis by Alaybek et al., 2022). Specifically, peak-end effects have been shown to strongly influence judgement of sequences, including series of rewards or events (Ross and Simonson, 1991; Ariely, 1998; Chapman, 2000; Lau-Gesk, 2005).

Among studies on the peak-end rule, "end effects" are the most frequently described. People tend to prefer experiences with positive endings (Loewenstein and Prelec, 1993; Diener et al., 2001; Just et al., 2015), or sequences that improve over time (Ariely, 1998; Chapman, 2000; Lau-Gesk, 2005). End effects are likely more prevalent because they are easier to test, whereas identifying peaks, as the most intense moments of an experience, can be more challenging. Additionally, the strong impact of endings on judgement and memory may be attributed to recency effects, arising simply from being experienced last (Ebbinghaus, 1885). Intriguingly, multiple studies have shown that a less favourable end can lower the perceived value of an otherwise superior experience. For instance, in the classic study by Kahneman et al. (1993), participants preferred to repeat a longer cold-water trial with a less painful ending over a shorter, consistently painful one. Similarly, Schreiber and Kahneman (2000) showed that adding a milder final segment to an unpleasant episode led to a more favourable overall memory, even though total discomfort increased. For positive experiences, people rated a happy life ending abruptly as better than a similar one extended with mildly happy years, despite having more total pleasure (Diener et al., 2001). Do et al. (2008) found that adding a lower-quality gift to a high-quality gift reduced satisfaction compared to receiving only the high-quality gift, despite the increase in total value.

However, very few studies have investigated peak-end effects in other animals. Research so far focused solely on primates, with inconsistent findings (Xu et al., 2011; Jung and Kralik, 2013; Blanchard et al., 2014; Egan Brad et al., 2016), but see a recent study on calves (Ede et al., 2023). Choices based on sequential experiences are especially relevant to nectarivores like bumblebees, which forage by moving from flower to flower within an inflorescence or flower patch, experiencing a sequence of rewards during each visit. Although prior experiences influence their foraging decisions (Dukas and Real, 1993; Biernaskie et al., 2009), whether bees are affected by peak-end effects when evaluating rewards and selecting flowers remains unknown. Notably, evidence for end effects in animals is inconsistent. Some studies showed that monkeys instead tend to choose sequences starting with high-value rewards over the reverse, indicating a preference for instant gratification (Xu et al., 2011; Jung and Kralik, 2013). Similarly, Ede et al. (2023) found no peak or end effects in calves' memory of pain. In contrast, Egan Brad et al. (2016) found that capuchins, like humans, tend to favour sequences ending with pleasurable rewards but do not intentionally structure events to maximize this effect. Blanchard et al. (2014) found that rhesus monkeys preferred sequences with high peak values and were especially sensitive to rewards at the end, to the extent that a small additional reward could decrease overall preference for the sequence. This aligns with previous findings on how a less satisfying end affects overall preference in humans.

The peak-end rule may be of direct ecological importance. Some animals, like bees, encounter sequential food rewards when foraging, requiring them to recall and evaluate flower options based on prior experiences for their subsequent foraging decisions. For instance, bumblebees assess each flower independently and adjust their choices based on reward variability and prior knowledge (Dukas and Real, 1993; Chittka et al., 2003; Biernaskie et al., 2009). Like humans, bees were also shown to be susceptible to recency effects (Prabhu and Cheng, 2008; Nityananda and Chittka, 2021). When foraging, bees rely on various heuristics to simplify decision-making. Bumblebees, for example, may use a simple "nearest-neighbour" rule, moving to the closest available flower (Ohashi et al., 2007; Saleh and Chittka, 2007). Alternatively, they may refine foraging routes through trial-and-error, reinforcing shorter paths and gradually creating efficient routes between flowers (Reynolds et al., 2013). In uncertain conditions, they have been shown to adopt a “copy-when-uncertain” heuristic, relying on social cues over personal information when nectar distribution is unpredictable (Smolla et al., 2016). In a study by MaBouDi et al. (2020), bumblebees trained to differentiate between larger and smaller shapes for a reward used a simple "win-stay/lose-switch" rule-of-thumb, improving their decision-making efficiency. In honeybees, the addition of an inferior option biased bees toward choosing an option similar to it, appearing more attractive by comparison—a heuristic known as the decoy effect (Shafir et al., 2002; Tan et al., 2014).

In nature, bees often forage on vertical inflorescences like foxgloves or wild sage, typically beginning at the lowest flowers and moving upward (Pyke, 1979; Waddington and Heinrich, 1979; Best and Bierzychudek, 1982). This behaviour results in a clear sequence of sub-events (individual flowers) per visitation event (inflorescence). Consequently, the overall perception of an inflorescence may be influenced by the order in which flowers with varying rewards are encountered. If the final flower contrasts poorly with the preceding ones, could it lower the perceived value of the entire inflorescence?

Here, we investigated whether bumblebees' preferences between two flowers were influenced by the quality of the final reward on each flower. Our experiment was inspired by the study of Do et al. (2008), who tested the peak-end rule in humans. In their experiments, participants who received a high-quality gift followed by a lower-quality one reported lower overall satisfaction than those who received only the high-quality gift, despite the second gift objectively increasing the total value. We trained individual *Bombus terrestris* bees on two distinct flowers, each offering a different sequence of nectar rewards: one with three high-quality (50% w/w) drops of sucrose solution, and the other with an additional lower-quality (20% w/w) sucrose solution drop. Although the second flower type offered a greater total amount of sucrose, we hypothesized that bees would prefer the flower associated with the sequence of three high-quality rewards, as it ends better than the sequence with a lower-quality final reward, despite its lower total sucrose value.

Material and Methods

Bees

Commercial *Bombus terrestris* colonies purchased from Koppert (The Netherlands) were used for the experiment. The bees were housed in plastic nestboxes (23 x 21 x 12 cm) which consisted of their original transport container, modified with a removable Plexiglas lid for easy handling of individuals. The colonies were kept under controlled laboratory conditions, maintained at 22–24°C with a 14:10 light:dark cycle, and with unlimited access to pollen. Each nestbox was connected to a flight arena (60 x 35 x 25 cm) via a transparent tube, leading to a small chamber (6 x 5 x 3 cm) equipped with shutters to regulate the movement of bees in and out of the nestbox. The bee selected for the experiment was allowed through a second tube connecting the chamber to the flight arena (see apparatus in **Fig. 1**). Between experimental sessions, bees had unrestricted access to the arena which contained six artificial flowers offering 20% w/w sucrose solution, replenished regularly throughout the day. Bees that regularly foraged on the flowers were marked on the thorax with uniquely numbered, coloured tags and selected for the experiment. A total of 71 bees were tested: 37 bees from three colonies between November and December 2022, and 34 bees from three additional colonies between April and May 2024 (see **Supplement S1** for further colony details).

Artificial flowers

Each artificial flower used in experiment consisted of a white plastic disc (diameter: 3.8 cm, thickness: 6 mm) topped with a 2 mm piece of coloured rubber foam. At the centre of each flower, a small opaque white resin cup (diameter: 4 mm, depth: 6 mm) was inserted into a pre-cut hole, and sucrose solution was pipetted into the cup (see **Fig. 1**). The flowers used during the experiment were either blue (with a peak reflectance at approx. 450 nm) or yellow (with a peak reflectance from approx. 540 to 700 nm, see reflectance curves in **Supplement S2**). Between experimental sessions, neutral white flowers were used to prevent the bees from associating experimental colours with sucrose rewards. The flowers were mounted horizontally into slits along the back wall of the flight arena, facing the entrance to ensure they were visible from the bees entering the foraging area. The wall contained a total of six slits arranged in three rows of two, with the lowest row positioned 5 cm above the arena floor and the highest row at 15 cm. Slits within the same row were spaced 6.5 cm apart (see **Fig. 1** below). To collect sucrose solution, the bees were required to fly to the flowers, land, and extract the solution from the resin cups.

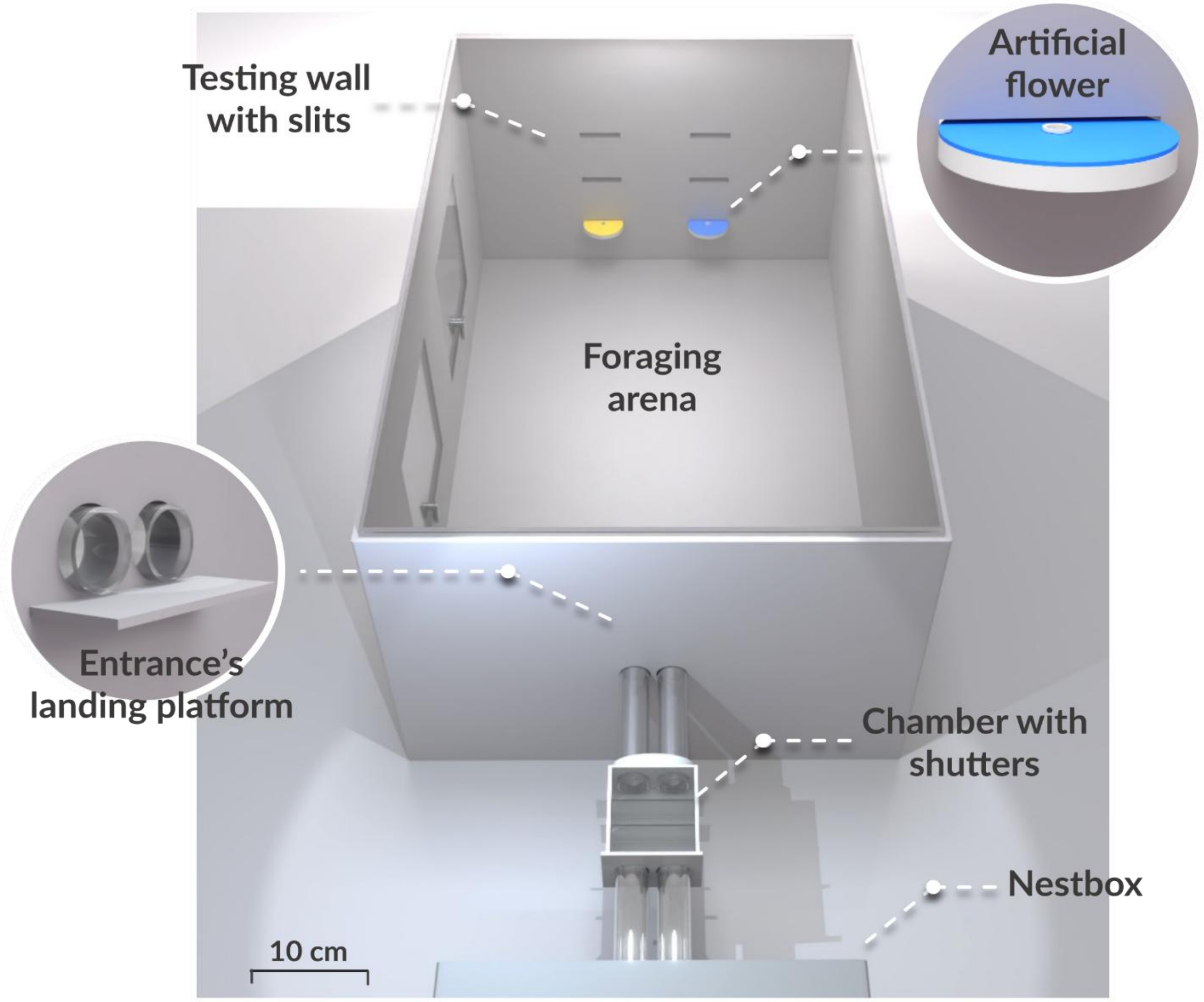

Figure 1: Top view of the scaled experimental setup. The 3D model (created in Blender) illustrates the final binary choice test, with the blue flower positioned on the right side and the yellow flower on the left, based on the bee's left-right orientation.

Main experiment

Individual bees completed twelve consecutive foraging bouts, with blue and yellow flowers presented alternately in each bout. Each flower type appeared six times before a final binary choice test, where both flowers were presented simultaneously. The flowers corresponded to two nectar reward sequences:

1. **Consistent sequence**: Three successive flowers (either all blue or all yellow), each offering 25 µL of high-quality (50% w/w) sucrose solution;
2. **Poor end sequence**: Three flowers identical to the consistent sequence, followed by a fourth additional flower offering 25 µL of lower-quality (20% w/w) sucrose solution.

This design ensured that bees experienced rewards sequentially. Each flower provided a total amount of sucrose solution per bout (75 µL for the consistent sequence and 100 µL for the poor end sequence), both below the average crop capacity of bumblebees (120–180 µL; Lihoreau et al., 2010), ensuring that all rewards could be collected by the bees.

At the start of each bout, the first flower was positioned in the lowest row of the wall, either in the left or right slit, ensuring its colour was clearly visible to the bee from above when entering the arena. Once the bee began collecting the reward, the second flower in sequence was gently inserted into the opposite slit by an experimenter stationed behind the arena. This process was repeated for the third flower, and for the fourth in the case of the poor end sequence (see video examples of bees foraging in **Supplement S3**). After the bee finished interacting with the final flower, the flower was removed, signalling the end of the bout and encouraging the bee to leave the arena. After each bout, all flowers were replaced with clean ones to prevent scent marks left by bees from affecting subsequent flower choices (Goulson et al., 2000; Saleh et al., 2007).

The positioning of the flowers (left/right slit) remained consistent across all twelve bouts for each bee, with the side order reversed for each flower type. For instance, blue flowers were always presented first on the left, while yellow flowers were presented first on the right. If a bee did not fully collect or engage with the fourth, lower-reward flower in the poor end sequence, it was allowed up to three probing attempts before the flower was removed, ensuring sufficient exposure to the lower-quality rewards. Notably, most bees (60 out of 71) rejected all lower-quality rewards, disengaging from the drops in less than a second (engagement time for a high-quality exceeded five seconds). However, every bee still probed the lower-quality drops in each bout.

After completing all twelve foraging bouts, the bee performed a final bout, where it had to choose between the two flower types placed side by side in the wall, both unrewarded. The flower positions remained consistent with the earlier bouts to help the bee anticipate each flower's location and reduce the likelihood of rushed or random choices. The first flower the bee landed on was recorded as an indicator of its preference.

Control experiment

A control experiment was conducted before the main trial to confirm whether the setup allowed bees to associate blue and yellow flowers with rewards. The setup mirrored the main experiment, but one flower type was associated with a sequence of three high-quality rewards (25 µL of 50% w/w sucrose solution), while the other was associated with three lower-quality rewards (25 µL of 20% w/w sucrose solution). This clear difference in reward quality allowed us to test whether bees could correctly identify and preferentially choose first the flower associated with the higher-quality reward sequence in the final test. All tested bees (n = 10) successfully landed first on the flower type associated with high-quality rewards during the binary choice test.

Data analysis

Each foraging bout was video-recorded using a Sony HDR-CX220 camera positioned above the flight arena. Bee behaviour was analysed using the event-logging software BORIS (v8.6). For each bee, we recorded: (1) reward collection (continuous licking of a sucrose solution drop for more than five seconds), (2) first flower visit (landing on the flower surface) in the binary choice test, and (3) all flower visits over a 1-minute period during the binary choice test.

Data processing was performed with Python (v3.11, Python Software Foundation, 2023) using the libraries *pandas* (McKinney, 2010) for data structuring, and *seaborn* (Waskom, 2021) and *Matplotlib* (Hunter, 2007) for data visualisation. Statistical analyses were conducted in R (v4.1, R Core Team 2022) using the *glmmTMB* package (Brooks et al., 2017) for Generalised Linear Mixed Models (GLMM), and *emmeans* (Lenth, 2020) for post-hoc tests. Model residuals were evaluated with the *DHARMa* package (Hartig, 2020). Datasets from both experimental sessions (2022 and 2024) were combined for analysis, with session treated as a random effect to account for variations in experimental conditions. Individual bees, nested within their respective colonies, were also included as random effects to control for intercolony variability. Potential confounding effects to sequence type, such as flower colour (blue or yellow), flower side (left or right slit in the arena), and flower exposure order (presented in the first or second foraging bout), were also tested for any influence on the bees' flower visits. Complete statistical analyses and datasets are available on Zenodo (https://doi.org/10.5281/zenodo.14068426).

Results

1. Flower colour influenced the bees' first flower choice

We first conducted a preliminary analysis to assess the influence of confounding flower factors on the bees' first visit during the binary choice test. Specifically, we examined whether the proportions of first visits differed by flower colour (blue or yellow), flower side (left or right), and exposure order (first or second). Among these factors, only flower colour showed significant differences in proportions, with bees visiting blue flowers more frequently than yellow flowers (binomial test: probability of visiting blue = 0.77, $p < 0.0001$, N = 71 visits).

Based on these results, we tested the effect of our variable of interest, the type of reward sequence (consistent sequence or poor end sequence), on the bees' first visit while controlling for flower colour. We found that the type of sequence did not significantly affect the bees' first flower choice, regardless of which colour it was associated to (GLMM, binomial family; yellow flowers: Intercept = 0.51, SE = 0.52, z = 0.99, *p* = 0.32; blue flowers: Intercept = 0.04, SE = 0.27, z = 0.13, *p* = 0.89, N = 71 visits). 62.5% of bees were likely to choose the consistent sequence flower when it was yellow, and 50.9% when the flower was blue (**Fig. 2A**). Although the probability of choosing the consistent sequence was higher when the flower was yellow, this effect was not significant (post hoc Tukey test: odds ratio = 1.61, SE = 0.936, z = 0.814, *p* = 0.415, N = 71 visits).

2. The interaction between flower colour and sequence type influenced overall flower visits

Next, we considered all flower visits made by the bees over a 1-minute period in the binary choice test. We examined the proportion of overall visits using the same factors as in 1). Only flower colour significantly affected choice proportions, with bees visiting blue flowers more frequently than yellow flowers (binomial test: probability of visiting blue = 0.60, $p < 0.0001$, N = 605 visits).

We then tested the effect of sequence type while accounting for the effect of flower colour. The bees visited significantly more flowers associated with the consistent rewards sequence when the flower was yellow (GLMM, binomial family: Intercept = 0.57, SE = 0.13, z = 4.26, $p < 0.0001$, N = 605 visits), but not when the flower was blue (Intercept = 0.13, SE = 0.11, z = 1.26, *p* = 0.209, N = 605 visits). When the consistent sequence was associated with yellow flowers, it accounted for 63.9% of visits, compared to 53.3% when associated with blue flowers (**Fig. 2B**). This difference was significant (post hoc Tukey test: odds ratio = 0.645, SE = 0.11, z = -2.577, *p* = 0.010, N = 605 visits).

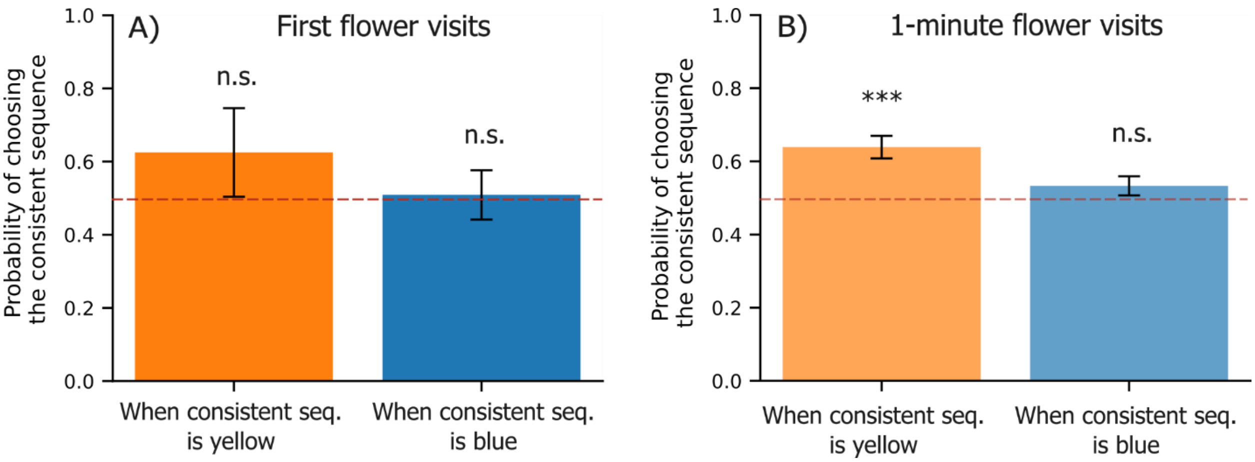

Figure 2: Predicted probabilities of visiting the consistent sequence flower for each flower colour. A: Proportion of choices in the first flower visit, when the consistent sequence flowers are blue or yellow (N = 71 visits); **B:** Proportion of choices across all flower visits over a 1-minute period, when the consistent sequence flowers are blue or yellow (N = 605 visits). Error bars indicate the standard errors of the predicted probabilities, and statistical significance is indicated as: ******* ($p < 0.001$), and **n.s.** ($p > 0.05$).

Discussion

This study examined whether bumblebees' preference between two flowers was influenced by the quality of the final reward received during a foraging bout on each flower type, assessing their susceptibility to order effects such as the peak-end effect. Contrary to our hypothesis, bees did not show a clear preference for the "consistent" flower with three high-quality rewards over the "poor end" flower with an additional, lower-quality reward at the end. Instead, their flower preference was largely driven by colour, with bees favouring blue flowers in both initial and overall visits during the binary choice test. However, tellingly, bees also did not favour the poor end sequence, despite its higher total value. We also note that, when considering all visits, bees showed a preference for flowers associated with the consistent sequence, but this was significant only when the flowers were yellow. Our results align with most findings on nonhuman animals, as studies in monkeys have shown inconsistent endpoint effects in preferences for food sequences (Xu et al., 2011; Blanchard et al., 2014; Egan Brad et al., 2016).

The lack of preference for the flower type with a higher total sucrose solution is intriguing and may reflect an endpoint effect, where a disappointing ending lowers the perceived value of an option. Similarly, in Kahneman et al. (1993), over one-third of participants did not favour the shorter trial with less total pain, nor did they prefer the longer trial with a less painful ending. Such absences of preference for the more profitable option are paradoxical and defy logical expectations. In fact, humans and animals have long been shown to deviate from normative rationality in their decision-making (Tversky and Kahneman, 1989; Shafir and LeBoeuf, 2002; Bateson et al., 2003). For instance, Solvi et al. (2022) demonstrated that bumblebees prioritise the remembered ranking of a flower's reward over its actual value, opting for flowers they recall as superior even when the rewards are equivalent.

In our experiment, most bees did not collect the lower-quality rewards in the poor-end sequence, even though the total volume of sucrose solution was well below their average crop capacity (Lihoreau et al., 2010). Furthermore, the quality of the "poor" reward (20% w/w sucrose solution) is considered adequate in natural flowers for bees (Pamminger et al., 2019), and we maintained the bees on this same 20% sucrose concentration in the lab. Foraging bees often reject downshifted rewards after experiencing higher-quality ones, a behaviour known as a negative incentive contrast effect (Bitterman, 1976; Waldron et al., 2005; Townsend-Mehler et al., 2011). Bumblebees, in particular, have been shown to quickly abandon a previously rewarding food source to seek out new food sources instead of returning to lower-quality options (Townsend-Mehler and Dyer, 2012). Although most bees in our experiment did not fully collect the downshifted flower, each bee still probed the extra reward, thus making them aware of the overall higher absolute value of this flower type, even if they chose not to take advantage of it. As an alternative to an order effect, this lack of preference might reflect an aversion to variability; studies show that bumblebees generally prefer flowers with consistent rewards, even when both options provide the same average reward

(Waddington et al., 1981; Harder and Real, 1987). The lower-value final reward may have made the flower type appear unpredictable or “risky”, further discouraging bees from choosing it.

Why did we not observe a clear preference for the consistent sequence over the poor end one? Our results suggest that any peak-end effect, if present, was likely small and largely masked by colour preference. We did find that bees tended to visit flowers associated with the consistent sequence more often, but this was statistically significant only over numerous visits and only when flowers were yellow, when colour preference was likely less influential. Bees have indeed a strong innate preference for blue flowers (Gumbert, 2000; Raine and Chittka, 2007), as reflected in our results. However, such preferences are flexible and can be reversed through learning (Gumbert, 2000). In our control experiment, where flowers had sharply contrasting reward qualities, bees consistently chose the highest-rewarding flower first, overriding their preference for blue.

Although bees showed a preference for consistent sequence flowers in their overall visits, this finding should be considered with caution. Since both flowers were unrewarded in the final binary choice test, bees likely checked the other flower after finding their preferred one empty, and repeated visits may reflect rushed or frustrated behaviour rather than genuine preference. However, similarly, Bortot et al. (2020) analysed honeybee preferences by evaluating total visits made within one minute rather than just the first visit, discovering a strong preference for one flower type that was not apparent in the initial choice. The cumulative choices animals make may thus reveal preferences that their initial choices do not show.

The main challenge in demonstrating peak-end effects in nonhuman animals likely stems from the methodology used to test such biases. In classic experiments, people evaluate experiences retrospectively (e.g. Kahneman et al., 1993; Ariely, 1998; Do et al., 2008), where participants are asked to report their overall feelings about various options. This approach is difficult to implement with nonhuman animals, which are typically required to choose their preferred options directly. For example, rhesus monkeys asked to select their favourite food sequence displayed a "peak-first" bias, preferring sequences that offer an immediate high-value reward over those that conclude with the most favourable one (Xu et al., 2011; Jung and Kralik, 2013). Egan Brad et al. (2016) found that human adults, children, and capuchin monkeys preferred sequences that ended with the most pleasurable reward; however, none of these groups intentionally structured events to enhance this end effect. In the study by Diener et al. (2001), where participants rated the desirability of fictional lives that ended either abruptly or were extended with additional years of mild happiness, they conducted an additional trial asking participants which life they would likely choose, rather than just rating them. They surprisingly found no preference for the shorter life that ended on a high note, despite favouring it in previous ratings. These findings illustrate a crucial distinction between retrospective evaluation and direct choice; the former relies on emotional state, whereas the latter is likely more influenced by immediate reward. Zauberman et al. (2006) reported that humans making more objective, analytical judgements are less affected by an experience’s emotional progression, weakening the peak-end effect. This type of processing may be relevant to nonhuman animals, like bees, where emotional behaviour is still under debate (see Baracchi et al., 2017b).

The question of whether bees are susceptible to peak-end effects is also ecologically relevant. In nature, bees often exhibit a bottom-to-top visitation pattern on vertical inflorescences (Heinrich, 1975; Waddington and Heinrich, 1979), giving each visit an "end." This stereotyped foraging behaviour is thought to help bees avoid costly flower revisits (Pyke, 1979; Best and Bierzychudek, 1982), similarly to traplining in flower patches (Cartar, 2004). If bees respond to peak-end effects, could this influence how nectar is distributed in plants? Floral structures are under selection and probably impacted by pollinator behaviour (Harder et al., 2004; Bailey et al., 2007). Concentrating rewards in top flowers could enhance perceived value while conserving energy, yet this pattern is not common across flowering plants. Conversely, many plants have their older, lower flowers producing higher nectar rewards than their newer, upper flowers (Waddington and Heinrich, 1979; Best and Bierzychudek, 1982). Moreover, studies that reversed the rewards order found that bees maintained their upward visitation pattern, even when top flowers offered the most nectar (Waddington and Heinrich, 1979; Corbet et al., 1981).

Bees typically reject and leave flower patches when the rewards decrease (Pyke, 1978; Heinrich, 1979). Specifically, Townsend-Mehler et al. (2011) showed that bumblebees are more likely than honeybees to abandon food sources that are decreasing in value and are quicker to discover new ones. Furthermore, bumblebees have been shown to leave flowers based on the nectar amount in the last flower probed (Cresswell, 1990) and often abandon an inflorescence when nectar levels drop below a certain threshold (Hodges, 1985). Such behaviour may benefit plants by encouraging pollinators to move to other flowers, thereby reducing the risk of self-pollination (Biernaskie et al., 2002). A better understanding on peak-end effects in foraging bees could offer new perspectives on nectar distribution patterns in plants and the co-evolution of plant-pollinator.

Supplementary Material

S1 contains the statistical analysis of the main experiment. **S2** provides the reflectance curves of the artificial flowers, and **S3** includes video clips of bees foraging. The dataset for the experiment is provided in **S4**. Full statistical analyses and datasets for all experiments are also available on Zenodo (https://doi.org/10.5281/zenodo.14068426).

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Chapter 4 – No decoy effect in bees: rewardless flowers do not increase bumblebees’ preference for neighbouring flowers

Mélissa Armand[1], Leonhard Herrnberger[1], Clara Jung[1] and Tomer J. Czaczkes[1]

[1]Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

Abstract

Nectarless flowers are common among flowering plants, which often retain colour-changed, rewardless flowers instead of shedding them. Yet, how these flowers influence pollinators' foraging choices within an inflorescence remains unclear. We hypothesised that rewardless flowers in an inflorescence may act as “decoys”, causing the rewarding flowers in the inflorescence to be perceived as more valuable by contrast. Using artificial inflorescences, we presented individual bumblebees (*Bombus terrestris*) with a binary choice between two equally rewarding inflorescences, one of which included additional unrewarded, differently coloured flowers. We found that the presence of rewardless flowers did not increase bees’ preference for neighbouring flowers, nor did it affect their overall choice between inflorescences. However, bees quickly learned to avoid the unrewarded flowers, drastically reducing visits and probing within a few foraging bouts. We review research on decoy effects in bees, and find very little support for their presence. Our findings contribute to the growing body of evidence that rewardless flowers do not induce decoy effects in bees, and highlight the need for further research into the ecological role of nectarless flowers within floral patches. It may be time to abandon the search for classical decoy effects in pollinators.

Introduction

Decision-making in animals is context-dependent: preferences arise from comparisons between available options, rather than from their only intrinsic value (Tversky, 1969; Tversky and Simonson, 1993; Rosati and Stevens; 2009; Owen et al., 2017). For example, a food reward may seem more appealing next to a poorer option, or a potentially acceptable mate may become irrelevant if a better one is available (Bateson et al., 2003; Wendt et al., 2019; Poissonnier et al., 2024). Such comparative evaluation can sometimes lead to seemingly “irrational” choices, where the chosen option is not objectively superior but appears favourable in context (Ariely, 2009).

One prominent example of this is the decoy effect, a cognitive bias where adding a clearly irrelevant, inferior option to a choice set shifts preferences among the remaining options (Huber et al., 1982). This phenomenon has been widely observed in both real-world contexts and experimental settings, affecting humans (Simonson and Tversky, 1992; Ariely, 2009; Marini et al., 2020) as well as non-human animals across diverse taxa, including mammals (Scarpi, 2011; Parrish et al., 2015; Jackson and Roberts, 2021), invertebrates (Shafir et al., 2002; Sasaki and Pratt, 2011; Hemingway et al., 2024) and even an unicellular organism (Latty and Beekman; 2011).

Flower-visiting insects navigate a multitude of floral options which differ in various traits that can be compared—a context particularly relevant to decoy effects, as reviewed by Latty and Trueblood (2020). Notably, many flowers within floral patches are naturally nectarless (Thakar et al., 2003). The persistence of such unrewarded flowers in plant populations remains unclear, as well as their potential impact on pollinator behaviour. Could these rewardless, irrelevant flowers act as decoys and influence the foraging decisions of pollinators?

Most decoy effects create an attraction effect, where the presence of an irrelevant decoy makes the option that most resembles it more appealing, shifting attention away from other options (Huber et al., 1982). The best studied example of this is the asymmetrically dominated (AD) decoy: clearly worse than a target option in one attribute but comparable to competitor options, making the target stand out as the best choice (Huber et al., 1982; Huber and Puto, 1983; Wedell, 1991). AD decoys have been shown in the context of foraging choices in pollinators: in honeybees, a decoy flower shifted preference towards flowers with deeper corollas over more concentrated nectar (Shafir et al., 2002) or towards flowers with a higher sucrose concentration over flowers offering warmer nectar (Tan et al., 2014b). In bumblebees, decoy effects were tested along two attributes, nectar concentration and reward rate, but an effect was only observed for reward rate (Hemingway et al., 2024).

Another class of decoys are phantom decoys: they create an attraction effect by introducing an option that appears desirable but is unavailable at the time of choice (Pratkanis and Farquhar, 1992; Trueblood and Pettibone, 2017). This unavailability leads decision-makers to favour the most similar alternative to their preferred, “sold out” option. Nectarless flowers in nature, for instance, may act as phantom decoys (Latty and Trueblood, 2020). However, few studies have examined the effect of empty flowers on pollinators in the context of a decoy effect, and findings are inconsistent. In honeybees, Tan et al. (2014a) found that an attractive but unavailable feeder increased preference for the most similar available option, whereas an unattractive phantom decoy had no effect. Conversely, Forster et al. (2023a) found that introducing an empty, previously rewarding flower did not shift bees’ preferences between the available flowers, and a similar lack of effect was observed in bumblebees (Forster et al., 2025).

In nature, pollinators tend to avoid unrewarding flowers (Cresswell, 1999; Smithson and Gigord, 2003) and spend less time on inflorescences containing empty flowers (Biernaskie et al., 2002; Hirabayashi et al., 2006). Rewardless flowers also increase bee movement between flowers and often lead to higher patch abandonment (Cresswell, 1990; Ishii et al., 2008; Nakamura and Kudo, 2016; Forster et al., 2023a). Yet, their influence on pollinator behaviour is ambiguous. Bees may prefer revisiting a known unrewarding flower over exploring an unfamiliar flower colour (Dyer and Murphy, 2009) and may be drawn to flowers with similar colours or attributes if they were previously rewarding (Internicola et al., 2007; Tan et al., 2015). Conversely, encountering empty flowers might instead push bees to seek out flowers with distinctly different colours (Smithson and Macnair, 1997; Smithson and Gigord, 2003).

Rewardless flowers are widespread among flowering plants (Thakar et al., 2003; Smithson and Gigord, 2003). Beyond the energetic cost of nectar production (Bell, 1986; Pyke, 1991), maintaining empty flowers may help reduce visitation of foragers to inflorescences, thereby limiting self-pollination between flowers (Thomson and Plowright, 1980; de Jong et al., 1993; Biernaskie et al., 2002). Among rewardless flowers, some never produce nectar (Gilbert et al., 1991; Gaskett, 2011), while others gradually decrease nectar production as they age (Weiss, 1991; Gilbert et al., 1991). Aging or pollinated flowers often change colour (Thakar et al., 2003; Brito et al., 2015) even within an inflorescence (see **Fig. 1A**), potentially signalling pollinators which flowers are unproductive (Weiss, 1991). Here, we propose an alternative hypothesis: that differentially coloured, unrewarding flowers may act as decoys, which by contrast causes the nearby productive flowers to be perceived as more valuable when compared to those in competing inflorescences. Successive contrast effects should also contribute to an increased preference for a rewarded flower experienced directly after experiencing an unrewarded flower (Bitterman, 1976; Wendt et al., 2019).

In this study, we investigated whether the presence of unrewarded flowers influenced the preference of bumblebees (*B. terrestris*) between two inflorescence options. To test this, we compared bees' overall preference between two equally rewarding inflorescences, one blue and one purple. In the control group, both inflorescences contained only rewarding flowers, whereas in the decoy groups, one inflorescence included two additional yellow, unrewarded flowers. We hypothesized that these differently coloured, rewardless flowers would act as decoys, enhancing the perceived value of neighbouring rewarding flowers by contrast. Therefore, we predicted that: (1) within groups, bees would prefer rewarding flowers in the inflorescence with decoy flowers, and (2) across groups, bees would have an increased preference for a given inflorescence (blue or purple) when it contained decoys, compared to when it did not.

Material and Methods

Colony setup

Commercial *Bombus terrestris* colonies were purchased from Koppert (The Netherlands) and kept under controlled laboratory conditions at 22–24°C with a 14:10 light:dark cycle. Colonies were housed in plastic nestboxes (23 × 21 × 12 cm), modified from their original transport containers with a removable Plexiglas lid for easy handling of the bees. Each nestbox was connected to its respective flight arena (60 × 35 × 25 cm) via a transparent tube leading to a small chamber (6 × 5 × 3 cm). The chamber featured a second tube that provided direct access to the arena and was fitted with transparent, removable shutters to regulate bee movement between the nest and arena (see apparatus **Fig. 2**).

Bees were provided daily with pollen balls made from a mixture of organic flower pollen pellets and 35% (w/w) sucrose solution, placed directly in the nestboxes. During the day, workers foraged freely on artificial inflorescences in the flight arena, which offered 35% (w/w) sucrose solution and were regularly refilled. A total of 92 bees participated in the experiment: 10 bees from three colonies in February 2023 and 82 bees from five colonies between October and November 2023 (see colony details in **Supplement S1**).

Artificial inflorescences

Bees foraged on artificial inflorescences mimicking an umbel, composed of small flowers symmetrically arranged in a circular pattern radiating from a central point (see **Fig. 1B**). Each flower consisted of an opaque cup (0.4 cm diameter, 0.6 cm height) filled with 35% (w/w) sucrose solution. The inflorescences were 3D-designed and printed using white resin and came in two sizes: 10-flower inflorescences (3.4 cm diameter, 5 cm height) and 12-flower inflorescences (4 cm diameter, 5 cm height). In the experiment, the 12-flower inflorescences included two additional unrewarded “decoy” flowers filled with plain water.

Flowers on all inflorescences were spaced 1 cm apart. To collect sucrose, the bees had to fly to an inflorescence, land, and extract the solution from the cups. Flowers were painted blue (peak reflectance ~470 nm), purple (peaks ~420 and ~670 nm), or yellow (weak peak from ~530–700 nm, see **Supplement S2** for reflectance curves). In the experiment, inflorescences were either all blue or all purple, with the decoy-equipped inflorescence containing two additional yellow decoy flowers. Blue and purple were used as colour cues for rewarding flowers because naïve bees naturally prefer them (Lunau, 1990; Gumbert, 2000), while yellow was chosen as a contrasting colour to clearly differentiate the decoy flowers from the neighbouring blue or purple flowers in the decoy inflorescences. Between experimental sessions, inflorescences were left unpainted in neutral white to prevent bees from associating experimental colours with rewards (see below).

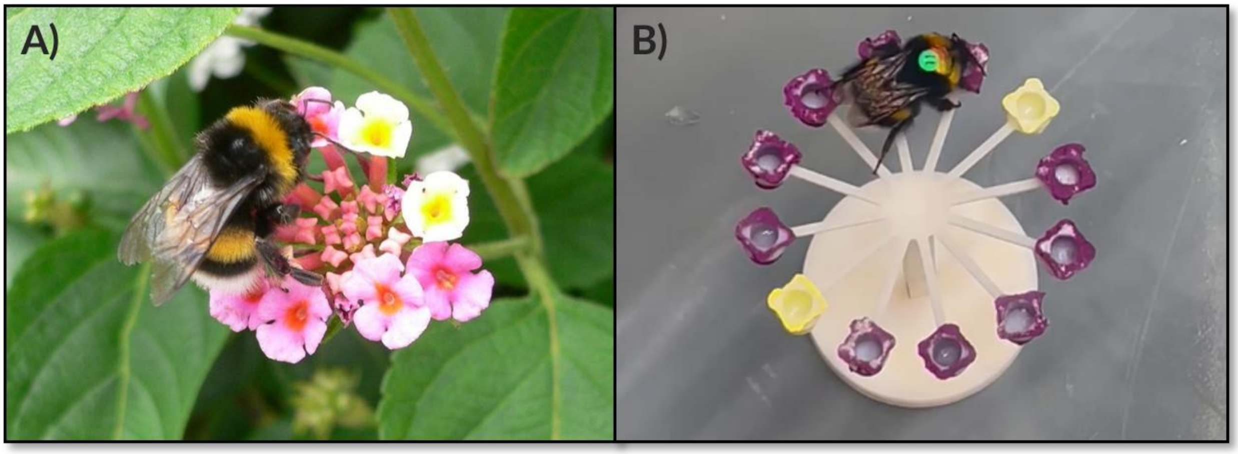

Figure 1: Bumblebee foraging on an inflorescence with differentially coloured flowers. A) Inflorescence of *Lantana camara*: newly opened, fertile flowers are yellow, while older, previously visited flowers turn orange to magenta due to anthocyanin accumulation triggered by pollination (Ram and Mathur, 1984). Photo © Luigi Strano; **B)** Artificial inflorescence used in experiment: purple flowers provided high-quality sucrose solution (50% w/w), while yellow flowers were rewardless and filled with plain water.

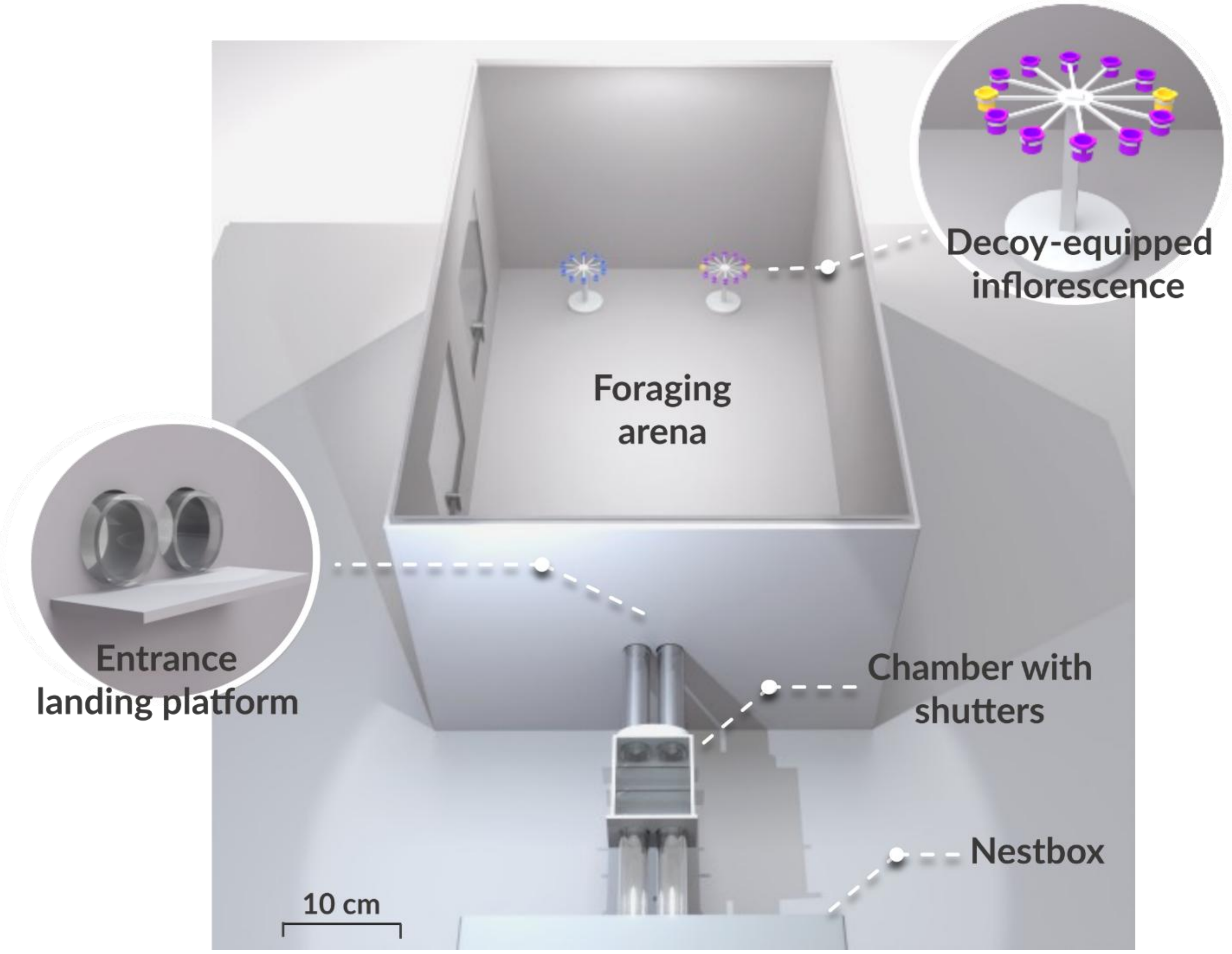

Figure 2: Top view of the experimental setup, to scale. The 3D model, created in Blender, illustrates a training bout featuring a purple, decoy-equipped inflorescence positioned to the right and a blue inflorescence to the left, as oriented from the bee's perspective.

Pre-training

Between experimental sessions, conducted in the afternoons from 1 to 4 pm, bees were allowed free access to the flight arena to familiarise themselves with the artificial inflorescences. The arena contained four all white inflorescences—two 10-flower and two 12-flower inflorescences—randomly positioned, to ensure bees were equally exposed to both sizes. Individual flowers were regularly replenished by an experimenter using a pipette through the arena's side doors. Bees observed foraging regularly on the inflorescences were captured and marked on the thorax with uniquely numbered, coloured tags, and considered for selection in the experiment on the same day.

Training

Bees remaining in the arena from pre-training were returned to the nestbox using forceps, the arena was wiped cleaned with 70% ethanol, and access was closed. When a tagged bee entered the chamber leading to the arena recording began, and training started. Bees were assigned to one of two treatments:

Control treatment (n = 31 bees): Bees were presented with two 10-flower inflorescences, one with all purple flowers and the other with all blue flowers. Each flower offered 4 μL of high-quality sucrose solution (50% w/w). This treatment tested the bees' relative preference between the purple and blue inflorescences, both of which offered the same total amount of sucrose.

Decoy treatments (n = 61 bees): Bees were presented with a 10-flower inflorescence (all purple or all blue) and a 12-flower inflorescence with 10 flowers of the other colour (purple or blue) plus two additional yellow, decoy flowers. Each flower contained 4 μL of high-quality sucrose solution (50% w/w), except the decoy flowers which were filled with 4 μL of plain water, effectively making both inflorescences equally rewarding. For 32 bees, the decoy-equipped inflorescence was blue ("Blue decoy" treatment) and for 29 bees, the reverse ("Purple decoy" treatment). These treatments tested whether the presence of decoy flowers influenced bees' relative preference between inflorescences compared to the control treatment.

Preferences were assessed at the population level by comparing treatment groups (control vs. decoys) rather than testing individual bees before and after introducing decoys. This approach avoided repeated trials with the same bees, eliminating the potential influence of prior exposure and learning effects.

The inflorescences were positioned at the centre of the arena, one on the left and one on the right, spaced 20 cm apart and 60 cm from the entrance. In the decoy treatments, decoy flowers were consistently placed on opposite sides within each inflorescence (left and right) to ensure their colour was clearly visible to bees entering the arena (see **Fig. 2**). Each bee was randomly assigned a colour and side for each inflorescence type, and these assignments were kept consistent across all bouts to help bees associate each inflorescence with visual and location cues.

In each foraging bout, both inflorescences provided a total of 80 μL of sucrose solution, which is below the average crop capacity of bumblebees (120–180 μL; Lihoreau et al., 2010), ensuring that all rewards could be collected. Inflorescences were replaced with clean ones each new bout to prevent scent marks from influencing subsequent foraging (Goulson et al., 2000; Saleh et al., 2007). Bees were required to probe at least one decoy flower (i.e., extend their proboscis into the cup) during the first bout to continue in the experiment.

Video analysis revealed that bees systematically walked on the surface of the inflorescence between neighbouring flowers, collecting them sequentially before switching to the second inflorescence, after fully depleting the first (see video example in **Supplement S3**). To ensure bees associated yellow flowers with the absence of reward, the decoys were filled with plain water rather than left empty. Pilot trials showed that empty decoys were treated as already-depleted flowers, with bees walking over them without probing, which could weaken the decoys' intended effect.

Binary choice test

After completing all six foraging bouts, each bee performed a final test bout with two inflorescences (purple vs. blue), both unrewarded (plain water) and without decoys. The positions of the inflorescences were kept consistent with earlier bouts to help the bees anticipate each inflorescence location and minimise rushed or random choices. We recorded the first inflorescence choice as an indicator of its preference.

Data analysis

Each foraging bout was video-recorded by a camera (Sony HDR-CX220) positioned above the flight arena. Bee behaviour was analysed using the event-logging software BORIS (v8.6). For each bee, we recorded in every foraging bout: (1) the first inflorescence visited (blue or purple; decoy-equipped or not), (2) the first flower landed on within the inflorescence (blue, purple, or yellow), and (3) whether a decoy flower was probed (i.e., bee's proboscis extended into the cup).

We tested the hypothesis that the presence of decoy flowers would change bees' relative preference between the blue and purple flowers, by comparing (1) the overall preference for each inflorescence in the control treatment to those in the decoy treatments, and (2) the preference for each inflorescence within treatments. We built a generalized linear mixed model (GLMM) with the first inflorescence choice (blue or purple) in the binary test as the response variable, and treatment ("control", "blue decoy" or "purple decoy") and inflorescence side ("left" or "right") as predictors. Random effects included bee colony and experimental session, and the model was fitted using a binomial distribution. We examined whether the estimated proportions of first inflorescence choice differed between treatments using post hoc pairwise comparisons with a Tukey correction. Additionally, we tested whether the estimated proportions within each treatment differed from a 0.5 probability using a post hoc Wald z–test.

We then tested whether probing a decoy flower increased the likelihood of bees first visiting the decoy-equipped inflorescence in the next bout, favouring nearby rewarded flowers over those of the other inflorescence. We used a GLMM with a binomial distribution, with inflorescence choice (1 for the decoy-equipped inflorescence, 0 otherwise) as the response variable. The fixed effects included whether a decoy was probed in the previous bout (1/0), the foraging bout, and their interaction. Random effects included individual bees nested within their colony and experimental session. The binary test bout and all training bouts were included in the analysis except the initial bout, where decoys could not have been previously probed. Post hoc pairwise comparisons with a Tukey correction tested differences between conditions (decoy probed or not in the previous bout).

Lastly, we examined whether the frequency of decoy flowers probed varied across bouts during training. We built a GLMM with a binomial distribution, with decoy probings as the binary response variable (1 for probing, 0 otherwise), foraging bout as a fixed effect, and individual bees nested within their colony and experimental session as random effects. All training bouts were included in analysis except the first, as bees retained in the experiment were required to probe a decoy flower during the first bout. We performed Post hoc pairwise comparisons with a Tukey correction to test if the estimated proportions differed between bouts.

Data processing was performed with Python (v3.11, Python Software Foundation, 2023) using the libraries pandas (McKinney, 2010) for data structuring, seaborn (Waskom, 2021) and Matplotlib (Hunter, 2007) for data visualisation. Statistical analyses were conducted in R (v4.1, R Core Team 2022) using the glmmTMB package (Brooks et al., 2017) for GLMMs, and emmeans (Lenth, 2020) for post hoc tests. Model residuals were evaluated with the DHARMa package (Hartig, 2020). Complete statistical analyses and datasets are available on Zenodo (https://doi.org/10.5281/zenodo.14995342).

Results

Overall, 92 bumblebees were tested across all treatments, with 61 bees in the decoy treatments. We analysed 363 first visits from training bouts 2–6 and the binary test bout.

Effect of decoy flowers on floral preferences

The presence of unrewarded flowers had no impact on bees' preference between the blue and purple inflorescences (GLMM, binomial family; treatment: $X^2 = 1.23$, df = 2, $p = 0.54$), and no effect of inflorescence side was observed (side: $X^2 = 0.0006$, df = 1, $p = 0.98$). The likelihood of first visiting either inflorescence in the binary test did not differ between treatments (post hoc Tukey test: control vs. decoy blue, odds ratio = 0.69 ± 0.38, z = -0.68, $p = 0.77$; control vs. decoy purple, odds ratio = 0.53 ± 0.30, z = -1.10, $p = 0.51$; decoy blue vs. decoy purple, odds ratio = 0.78 ± 0.43, z = -0.45, $p = 0.89$; **Fig. 3**) or within treatments (post hoc Wald *z*-test: control: log-odds = -0.50 ± 0.46, z = -1.07, $p = 0.28$; decoy blue: log-odds = -0.12 ± 0.47, z = -0.26, $p = 0.79$; decoy purple: log-odds = 0.13 ± 0.42, z = 0.31, $p = 0.76$).

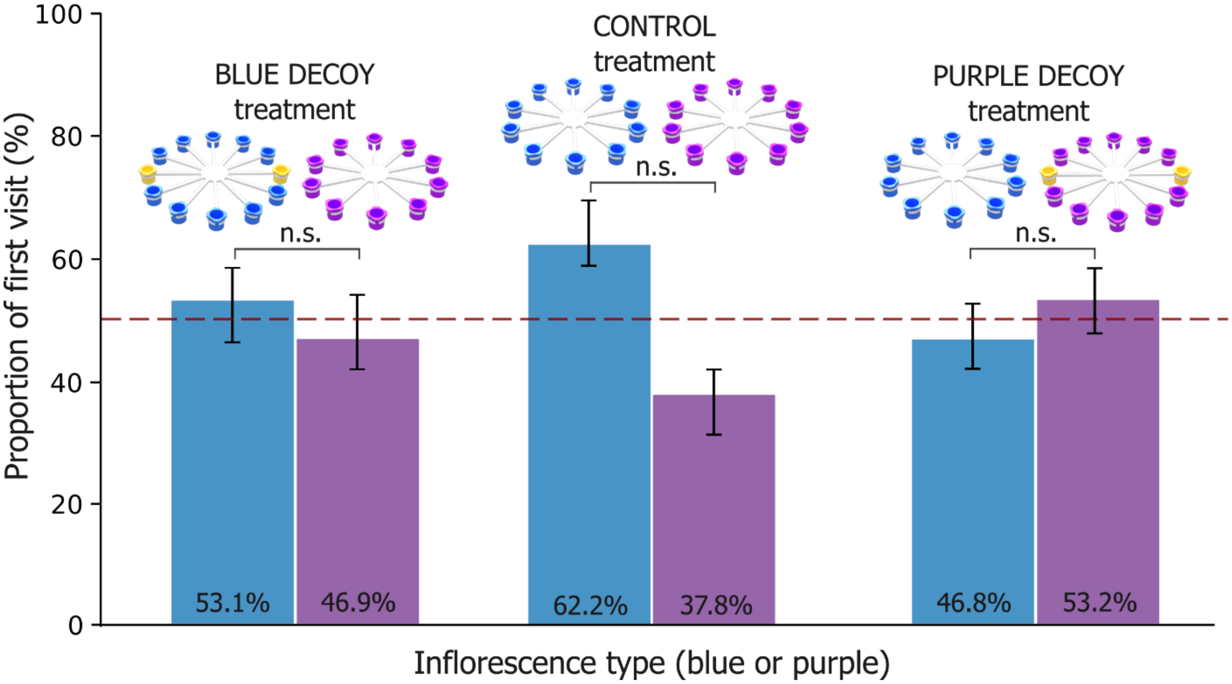

Figure 3: Estimated probabilities of first visits in the binary test across treatments. Probabilities were derived from the GLMM and calculated through post hoc analysis. Error bars represent the standard errors of the predictions. Statistical differences within treatments are indicated as **n.s.** ($p > 0.05$).

Effect of probing a decoy flower on floral preferences

Probing an unrewarded flower did not affect bees' preference between the blue and purple inflorescences in the next foraging bout (GLMM, binomial family; probed decoy: $X^2 = 1.34$, df = 5, $p = 0.93$). Preferences did not differ across bouts (foraging bout: $X^2 = 5.47$, df = 9, $p = 0.79$), nor did the effect of probing a decoy vary with foraging bout (interaction: $X^2 = 1.33$, df = 5, $p = 0.93$). The likelihood of first visiting the decoy-equipped inflorescence was similar for bees that probed a decoy flower in the previous bout and those that did not (**Table 1**).

Foraging bout	**Condition (probed 1/0)**	**Estimated probability (± SE)**	**Odds ratio**	**95% CI**	***p-value***
Foraging bout 2	1	0.576 ± 0.1	/	/	/
Foraging bout 3	0	0.522 ± 0.1	0.819	(0.271, 0.763)	0.753
	1	0.572 ± 0.1			
Foraging bout 4	0	0.420 ± 0.1	0.986	(0.233, 0.637)	0.981
	1	0.423 ± 0.1			
Foraging bout 5	0	0.551 ± 0.1	0.678	(0.369, 0.720)	0.564
	1	0.644 ± 0.1			
Foraging bout 6	0	0.634 ± 0.1	1.830	(0.438, 0.794)	0.347
	1	0.487 ± 0.1			
Binary test bout	0	0.503 ± 0.1	1.087	(0.329, 0.677)	0.904
	1	0.483 ± 0.2			

Table 1: Estimated probabilities of first inflorescence choices and pairwise comparisons across bouts. Estimated probabilities are of first visits to the decoy-equipped inflorescences, based on the GLMM model. Odds ratios, 95% confidence intervals (CI), and p-values refer to pairwise comparisons between conditions (whether a decoy flower was probed in the previous bout or not).

Frequency of interactions with decoy flowers across bouts

Bees quickly learned to avoid unrewarded flowers: foraging bout significantly affected the likelihood of probing decoy flowers (GLMM, binomial family; foraging bout: $X^2 = 32.83$, df = 4, $p < 0.0001$). Bees were less likely to probe unrewarded flowers in later bouts compared to earlier ones (**Fig. 4**). Additionally, of the 363 first flower landings recorded across all training bouts, 15 were on decoy flowers in the first bout (26% of landings in that bout), compared to just 2 across all subsequent bouts combined (0.7% of landings).

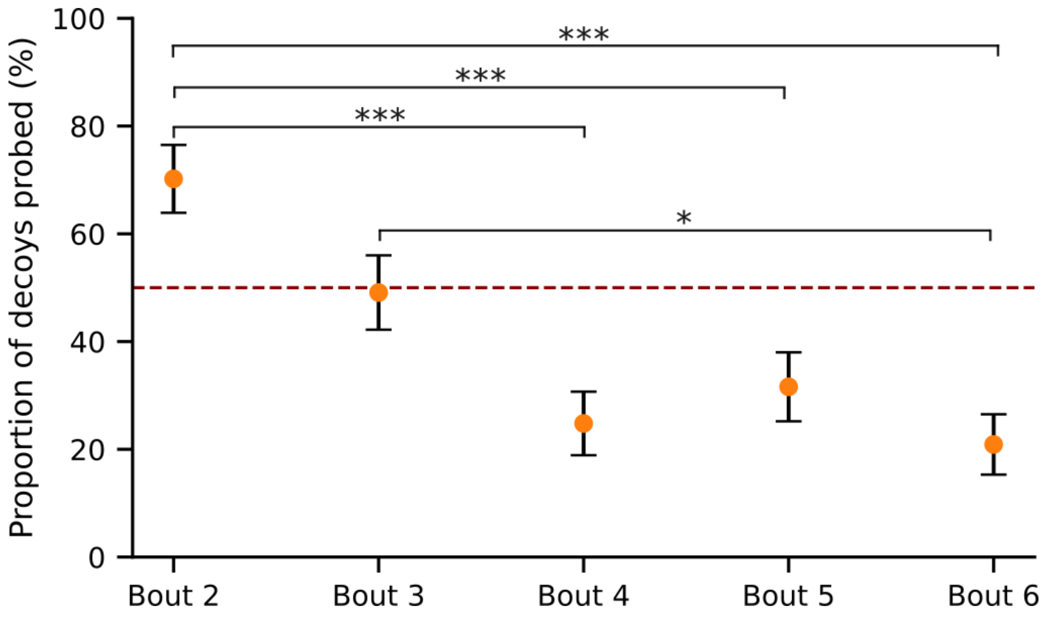

Figure 4: Estimated proportions of probing a decoy flower across foraging bouts. Probabilities of probing a decoy flower in training bouts 2–6 were derived from the GLMM and calculated through post hoc analysis. Error bars represent the standard errors of the predictions. Statistical differences within treatments are indicated as ******* ($p \leq 0.001$), and ***** ($p \leq 0.05$).

Discussion

We tested whether rewardless yellow “decoy” flowers influenced bumblebees’ choice between two equally rewarding inflorescences, blue and purple. Contrary to expectations, unrewarded flowers did not increase bees’ preference for neighbouring flowers. In the binary choice test, bees showed no overall preference for either inflorescence. During training, those that probed a rewardless flower did not favour rewarded flowers in the same inflorescence in the next bout. However, bees quickly learned to avoid unrewarded flowers, reducing visits and probings over successive bouts.

A decoy effect would have caused the introduction of an irrelevant option to shift bees’ relative preference between existing choices (Huber et al., 1982). In that case, first inflorescence choice in the binary test should have increased for the blue inflorescence in the "decoy blue" treatment and for the purple inflorescence in the "decoy purple" treatment, relative to the control (see **Fig. 3**). Our findings align with those of Forster et al. (2023a, b; 2025), who found that the presence of empty, previously high-reward flowers did not influence bees’ foraging choices. In their honeybee experiment (Forster et al., 2023a), decoy flowers did not shift preference between the two available flowers but led to increased movement between flowers and higher patch abandonment. In their study on stingless bees, Forster et al. (2023b) found no preference for the flower option matching the colour of the decoy flower. In Forster et al. (2025), bumblebee foraging choices were tested in a social context rather than individually, as in our study. They found that social information was the primary driver of choice, with bees preferring flowers where conspecifics were present.

During training, probing an unrewarded flower did not make bees more likely to favour neighbouring rewarded flowers in the next bout. Instead, their likelihood of choosing either inflorescence first remained constant across bouts. This contradicts our hypothesis that an irrelevant option would create an attraction effect, making nearby rewarding flowers more appealing by comparison (Huber et al., 1982), thereby increasing bees' likelihood of foraging on these flowers rather than on similar ones in another inflorescence. However, it is important to note that rewardless flowers in our setup did not have a repulsion effect either: bees systematically collected all available sucrose rewards on an inflorescence before switching to the other, regardless of the presence of unrewarded flowers. By contrast, previous studies reported that rewardless flowers reduced pollinator visitation to an inflorescence (Cresswell, 1990; Smithson and Gigord, 2003; Forster et al., 2023b). Similarly, bumblebees were found to visit fewer flowers within an inflorescence when some were empty (Biernaskie et al., 2002; Smithson and Gigord, 2003; Nakamura and Kudo, 2016).

While unrewarded flowers did not influence foraging choices, bees in our experiment quickly learned to associate them with the absence of rewards. In decoy treatments, one-quarter of first landings were on unrewarded flowers in the initial bout, dropping to less than 1% over the next five training bouts. Bees also progressively reduced their probing of rewardless flowers across successive bouts. Extensive research showed that bees readily associate colours with rewards (Heinrich, 2004; Raine and Chittka, 2008) and recall spatial landmarks (Menzel et al., 1996), as seen in our setup where unrewarded yellow flowers remained in a fixed position across bouts. Similarly, studies have shown that bees quickly reduce visits to newly depleted flowers (Forster et al., 2023b; 2025), avoid unattractive food sources (Tan et al., 2014a), and minimise handling time of empty flowers (Smithson and Gigord, 2003).

In the control treatment without decoy flowers, bees tended to choose the blue inflorescence first more often than the purple one despite both being equally rewarding (**Fig. 3**), but this preference was not significant. While bees have innate preferences for violet and blue flowers (Gumbert, 2000; Raine and Chittka, 2007), our purple flowers had lower spectral purity than the blue ones due to additional reflectance in the red range (see curves in **S2**), which likely reduced their saliency in the arena (Lunau, 1990). High spectral purity enhances floral attractiveness to bees (Lunau et al., 1996; Gumbert, 2000), which may explain the slight preference for blue. However, this tendency disappeared in the decoy treatments; we suggest that the presence of yellow flowers increased visual complexity, mitigating any subtle colour biases.

First visits to the yellow, unrewarded flowers were notably high (25%) during the first bout, despite their low abundance — only two (10%) among 20 blue and purple flowers in the arena. This may be due to their visual similarity to the white flowers used in pre-training, which bees had positively associated with rewards. Since the bees were colour-naïve in the initial bout, they may have perceived the yellow flowers as familiar. Bumblebees typically show a preference for novel colours that resemble those they have previously encountered (Gumbert, 2000).

While bees gradually reduced their probing of unrewarded flowers, they did not stop entirely. Instead, probings stabilised in later bouts rather than declining to zero, suggesting that bees continued to inspect them intermittently, albeit less frequently. Video analysis confirmed this pattern, showing that individual bees frequently re-probed rewardless flowers in a later bout even though they ignored them in previous ones. Similarly, Forster et al. (2023a) found that bees revisited empty flowers, possibly anticipating nectar replenishment. Ishii et al. (2008) noted that while bumblebees frequently re-inspected rewardless flowers, they re-probed them less often. In nature, bees commonly revisit depleted flowers probably due to memory constraints (Chittka et al., 1999).

Is it surprising that we found no clear decoy effect in our experiments, when they are apparently commonly reported? A closer look at the literature reveals that clear evidence for decoy effects is often lacking. For instance, studies testing asymmetrically dominated (AD) decoys in bees have failed to demonstrate attraction effects. In Shafir et al. (2002), where AD decoys were tested in honeybees and grey jays, only grey jays showed a true decoy effect. In bees, the decoy flower reduced choices for the competitor more than the target option, shifting relative preference, but this resulted from direct selection of the decoy rather than an increased attraction to the target. Similarly, Tan et al. (2014b) found that an AD decoy redirected choices from the competitor without increasing honeybees' preference for the target food option. Hemingway et al. (2024) tested an AD decoy in bumblebees and found that adding a lower-concentration flower increased preference for the target, a medium-concentration flower. However, this shift likely resulted from an incentive contrast: rather than enhancing the perceived value of the medium option, exposure to the lower-quality alternative merely lowered the bees' acceptance threshold. Incentive contrast effects are well documented in bees, which often reject lower-quality rewards after experiencing higher-quality ones (Bitterman, 1976; Waldron et al., 2005; Townsend-Mehler et al., 2011). To our knowledge, the only example of a true decoy effect in insects was reported by Sasaki and Pratt (2011), who presented individual ants and whole colonies with two equivalent but different nest sites: one with a small entrance (preferred) but too bright, and the other dark (preferred) but with an overly large entrance. Individual ants shifted their preference toward the nest superior to the decoy nest they had previously experienced, whereas whole colonies showed no decoy effect. This is an important study, though we note the modest sample sizes of 12 and 14 ants per decoy treatment.

Likewise, previous studies testing phantom decoys in pollinators have been mostly inconclusive. Recent work by Forster et al. (2023a, 2023b, 2025) showed that empty flowers had no effect on preference or choice in several bee species. Tan et al. (2014a) found that while a few honeybees shifted toward the option most similar to an attractive phantom decoy, there was no consistent effect at the group level. The authors suggest this shift was due to incentive contrast, similarly to Hemingway et al. (2024): some bees that expected a high reward but found nothing lowered their selectivity and settled for a lower-quality alternative, rather than being drawn toward the most similar available option as predicted in a true decoy effect. Moreover, they found that an unattractive phantom decoy did not affect bee choice, instead of making the similar, still-available option look better in comparison and thus increase its selection rate.

The robustness of attraction effects has been increasingly questioned in recent years (Frederick et al., 2014; Yang and Lynn, 2014; Evans et al., 2021). Frederick et al. (2014) replicated 38 human studies on AD decoys but failed to reproduce most findings; they found attraction effects only when options were compared numerically, rather than experienced directly. The authors argued that in realistic settings, direct experience weakens structured comparisons, making dominance relationships less apparent. Additionally, attraction effects may diminish or disappear when decisions are made under time constraints, as often occurs in real-world situations (Pettibone, 2012; Marini et al., 2023). This issue is particularly relevant for nonhuman animals, where decoy effects can only be tested through direct choices. In fact, numerous studies on decoy effects in nonhuman animals had mixed or partial results (Bateson et al., 2003; Scarpi, 2011; Pinto et al., 2016; Marini et al., 2023), or found no evidence of a decoy effect at all (Bateson, 2002; Edwards and Pratt, 2009; Cohen and Santos, 2017; Parrish et al., 2018). To our knowledge, there is currently no clear demonstration of a decoy effect in pollinators.

Could unrewarded flowers induce repulsion effects on neighbouring flowers instead? Flower-visiting insects have been shown to visit fewer flowers within inflorescences containing empty flowers (Biernaskie et al., 2002; Ishii et al., 2008), or even avoid patches entirely when rewardless flowers are abundant (Hirabayashi et al., 2006; Nakamura and Kudo, 2016). Notably, some decoy studies have reported repulsion effects, suggesting that a decoy option can make the target appear less desirable, as the negative perception of the decoy “contaminates” the target (Frederick et al., 2014). Spektor et al. (2018) found that such repulsion effects emerge when the decoy and target options are closely located, with their proximity triggering a similarity effect between them.

Despite their potential repulsive effects, a balanced proportion of nectarless flowers may be beneficial to plants (Bell, 1986). Bees prefer larger inflorescences over smaller ones (Hirabayashi et al., 2006; Ishii et al., 2008), so bearing rewardless, “cost-free” additional flowers may enhance the attractiveness of an inflorescence (although we found no evidence for this in our study). Moreover, fewer visits per inflorescence due to the presence of nectarless flowers can help reduce selfing, limiting inbreeding and thereby, enhancing plant fitness (de Jong et al., 1993; Biernaskie et al., 2002).

In summary, we found that the addition of rewardless flowers did not increase bees’ preference for nearby rewarded flowers. While not a classical asymmetrically dominated decoy study, the experiment shared many elements with such studies, and has direct ecological relevance to rewardless flowers on inflorescences. Bees rapidly adapted to the presence of rewardless flowers, reducing the time spent visiting and probing them after just a few foraging bouts. A sizeable body of research is accumulating, suggesting that classical decoy effects do not play a significant role in insect foraging, and thus decoy-like effects cannot explain the presence of nectarless flowers. Further research is needed to clarify the effect of nectarless flowers on the attractiveness of surrounding flowers. While decoy and decoy-like effects attract a lot of research attention, evidence for them is weak and inconsistent, and it may be time to redirect research attention to other valuation illusions.

Supplementary Material

S1 contains the statistical analysis of the main experiment, **S2** provides the reflectance curves of the artificial inflorescences, **S3** includes a video clip of a bee foraging during the experiment, and **S4** the dataset. All supplementary materials are available on Zenodo (https://doi.org/10.5281/zenodo.14995342).

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Chapter 5 – Robotic flowers for testing bee foraging behaviour: a system overview and implications for investigating cognitive biases

Mélissa Armand[1], Massimo De Agrò[2] and Tomer J. Czaczkes[1]

[1]Animal Comparative Economics Laboratory, Department of Zoology and Evolutionary Biology, University of Regensburg, 93053 Regensburg, Germany

[2] Center for Mind/Brain Sciences, University of Trento, Trento, Italy

Abstract

Classical economic models propose that individuals make consistent, utility-maximising decisions. However, animals such as bees often violate these rational principles in their foraging behaviour, instead relying on simple decision rules, or heuristics, that can give rise to cognitive biases: systematic errors in how they evaluate options and make choices. While well documented in humans, such biases remain rarely explored in invertebrates, partly due to the difficulty of testing them. To address this gap, we developed an automated flower system for lab-based experiments on bee foraging. We present a system overview of its prototype and test its potential in a pilot experiment on bumblebees (*Bombus terrestris*). The artificial flowers are fully programmable, capable of delivering tailored sucrose rewards to individual bees and continuously recording flower choices over extended periods, with minimal human intervention. We outline key advantages of the system for studying cognitive biases and propose concrete directions for future experiments. As technologies rapidly transform insect behaviour research, programmable feeders that manipulate foraging conditions are becoming essential tools for understanding how individuals perceive, evaluate, and choose between food options.

Introduction

Decision-making often occurs under uncertainty or limited resources, prompting individuals to rely on heuristics: simple "rules of thumb" that reduce cognitive effort and enable fast, good-enough decisions (Simon, 1955; Tversky and Kahneman, 1974; Gigerenzer, 2021). While generally adaptive, heuristics can sometimes lead to systematic errors in judgement known as cognitive biases (Tversky and Kahneman, 1974; Shafir and LeBoeuf, 2002). These predictable distortions in perception or reasoning often result in suboptimal decisions, challenging the notion of rational behaviour central to classical economic models (von Neumann and Morgenstern, 1944; Luce and Raiffa, 1957).

Many invertebrates were shown to rely on heuristics to solve complex tasks. For example, desert ants approximated vector calculations to return to their nest, tolerating small systematic errors (Müller and Wehner, 1988). Honeybee scouts initially performed longer waggle dances for higher-quality nest sites, then gradually reduced dance intensity to eliminate poorer options (Seeley, 2003). Rather than comparing all sites, honeybees used a quorum threshold rule—committing to the first site that reached a critical number of scout visits (Seeley and Visscher, 2003; 2004). Ant scouts estimated nest size by counting intersections with their own pheromone trails (Mallon and Franks, 2000). Both ants and bees adjusted their foraging effort by using waiting time during food unloading as a simple cue to meet colony needs (Lindauer, 1955; Seeley and Tovey, 1994; Jeanne, 1999). In some cases, individuals employ embodied heuristics: simple rules that use the body itself as a reference. Spiders, for example, used leg length as a spatial guide when building webs (Vollrath, 1987), while tree crickets cut holes in leaves roughly the size of their wings (Mhatre et al., 2017). Insects also use heuristics in tool use (see review by Mhatre and Robert, 2018) and foraging (see **Table 2** in the **General Introduction** for examples in bees).

Yet, these simple decision rules can lead to seemingly irrational choices. In insects, most deviations from rationality have been observed in context-dependent decision-making. For example, desert locusts preferred food associated with past hunger, even when it no longer differed from other available options (Pompilio et al., 2006). Similarly, ants evaluated food based on prior experience, expectations, or social cues rather than its absolute quality (Wendt et al., 2019; Wendt and Czaczkes, 2020). Risk aversion can also lead to suboptimal choices, as shown in ants (De Agrò et al., 2021) and bees (Greggers and Menzel, 1993; Shafir et al., 1999). Another well-studied source of irrational choices in insects is judgement bias, where internal states affect how individuals perceive their options (Mendl et al., 2009; Bateson, 2016). For instance, stress induced pessimism in bees and ants, reducing their willingness to approach ambiguous cues (Bateson et al., 2011; Schlüns et al., 2017; Procenko et al., 2024). In contrast, unexpected sucrose rewards made bees more optimistic and more likely to respond to ambiguous stimuli (Solvi et al., 2016; Strang and Muth, 2023). Deviations from rational behaviour have been most frequently observed in foraging bees (see examples in **Table 3** in the **General Introduction**).

Despite growing evidence that heuristics and biases influence decision-making, they remain understudied in insects. In particular, few studies have tested classic cognitive biases well established in humans (but see review by Latty and Trueblood, 2020). Evidence for cognitive biases in nonhuman animals is often mixed and difficult to replicate. For instance, both the peak-end effect and the decoy effect have yielded conflicting findings in primates (refer to **Chapters 3** and **4**). In insects, the decoy effect illustrates this inconsistency: one study found clear evidence for it in ants (Sasaki and Pratt, 2011), while others reported mixed results (Shafir et al., 2002; Tan et al., 2014; Hemingway et al., 2024) or null results (Forster et al., 2023a; 2023b; 2025). These discrepancies highlight the importance of experimental design and suggest that methodology plays a critical role in detecting cognitive biases.

While studying decision-making in nonhuman animals presents methodological challenges (Marsh, 2002), especially in insects, emerging technologies are rapidly transforming insect behaviour research. In field experiments on bees, for example, Radio Frequency Identification (RFID) systems use tiny tags glued to the thorax of foragers, which are detected by antennas placed at checkpoints such as nest entrances or feeders. This method generates precise data on foraging frequency, duration, and flower choices (Orbán and Plowright, 2014b; Russell et al., 2017; Gomes et al., 2020). Harmonic radar, by contrast, uses lightweight transponders to track free-flying insects over larger distances, enabling real-time mapping of flight paths (e.g. Woodgate et al., 2016; Makinson et al., 2019). More recently, computer vision (CV) systems have enabled continuous, non-invasive behavioural monitoring, by combining cameras with machine learning to automatically detect and track untagged insects. For instance, Tu et al. (2016) used CV to track unmarked honeybees at hive entrances in real time, while Ratnayake et al. (2021) and Haalck et al. (2023) combined CV with deep learning to track untagged bees and ants in outdoor environments.

While these technologies provide detailed behavioural data and enable individual tracking, they remain largely observational and offer limited control over the stimuli experienced by individuals. Among emerging tools, automated feeders are particularly promising for testing cognitive biases in insects, notably in foraging bees. For example, Kuusela and Lämsä (2016) developed a low-cost robotic flower system that detects bee visits using sensors and delivers realistic, programmable sucrose rewards. The volume and timing of each reward can be precisely controlled, and the flowers refill automatically. More recently, Debeuckelaere et al. (2024) developed similar robotic flowers with wireless, remotely operable features, making it suitable for long-term experiments in the field. These robotic flowers can also mimic natural variability in nectar availability through programmable refill patterns. Such automated feeders could be adapted to further investigate decision-making in foraging bees, notably to reveal cognitive biases.

Here, we present a prototype of a robotic flower system designed to test bee foraging behaviour. We conducted a pilot experiment to evaluate the system's reliability and assess whether bumblebees (*Bombus terrestris*) could learn to forage from these artificial flowers. Bees were given access to four flowers, two blue and two purple, and were randomly assigned to one of two groups with opposite reward conditions. Bees in group A received 10 µL of high-quality sucrose solution (40% w/w) from blue flowers and 10 µL of low-quality solution (15% w/w) from purple flowers, while group B experienced the reverse. We predicted that bees would favour the high-quality flowers during their foraging trips by visiting them more frequently. We present preliminary results and discuss the broader potential of automated flowers for investigating decision-making in bees, suggesting specific cognitive biases that could be tested using this system.

Material and Methods

Colony setup

A commercial *Bombus terrestris* colony was purchased from Koppert (The Netherlands) and maintained under controlled laboratory conditions at 22–24°C with a 14:10 light:dark cycle. The colony was housed in a plastic nestbox (23 × 21 × 12 cm), adapted from its original transport container with a removable Plexiglas lid for easy handling of the bees. The nestbox was connected to a large flight arena (95 × 75 × 50 cm) via a transparent tube fitted with transparent, removable shutters to regulate bee movement between the nest and arena.

Bees were provided daily with pollen balls made from a mixture of organic flower pollen pellets and 15% (w/w) sucrose solution, placed directly inside the nestbox. During the day, workers foraged freely in the flight arena on six artificial flowers, each consisting of a transparent plastic cup topped with a white cap. The flowers provided *ad libitum* sucrose solution (15% w/w) through damp cotton meshes, which were soaked in solution inside each cup and protruded through a central hole in the cap.

Robotic flower system overview

Each artificial flower (18 × 5.5 × 7 cm) is 3D-printed in white resin and is composed of six integrated components: an LED light with adjustable colours, a landing platform, a narrow slit leading to a feeder, a camera, a Raspberry Pi (i.e., single-board computer), and four peristaltic pumps (see apparatus in **Fig. 1**). In the flight arena, only the LED and landing platform are visible to foraging bees; the remaining components are concealed behind the arena wall, where the flowers are mounted (see arena in **Fig. 2**).

Each bee is identified by a unique tag (ArUco code), allowing the flowers to detect bees automatically via the camera positioned above the feeder. The Raspberry Pi then records parameters specific to each bee, including its colony origin, experimental group, and the designated volume and concentration of sucrose solution to be dispensed at the feeder.

Bees are attracted by the coloured LED on the front of the flower, which guides them to land on the platform and enter the narrow slit to access the feeder containing sucrose solution (see video examples in **Supplement S1**). Placed above the feeder, the camera continuously scans for tags to identify foragers. Upon detection, the camera relays the bee's information to the Raspberry Pi, which activates the peristaltic pumps to dispense the precise volume and concentration of sucrose solution through a tubing system.

The entire sequence, from detection to sucrose delivery, occurs within seconds. Foraging data, including flower entries and exits with corresponding timestamps, are recorded and transmitted in real time to a central hub computer, which centralises data from all flowers.

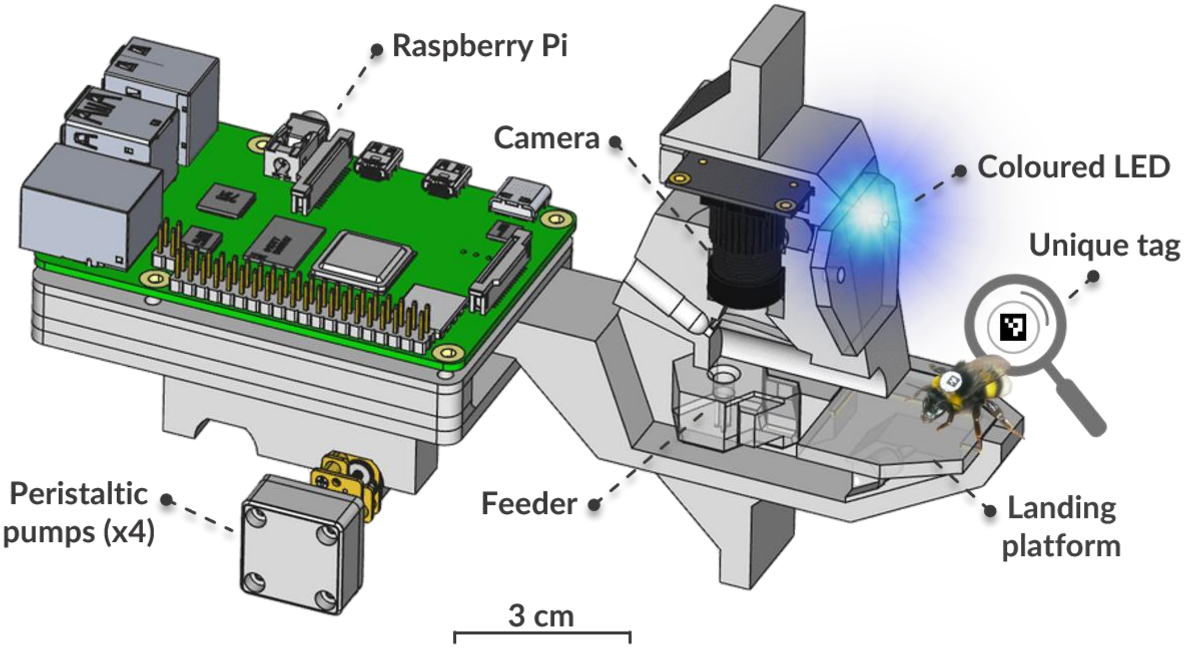

Figure 1: 3D schematic model of the cross-section of a robotic flower. The flowers are mounted on the back wall of the flight arena, with all components except the LED and landing platform concealed behind the arena wall. Tagged bees are attracted by the LEDs and enter the flower slits to access the feeders, which dispense sucrose solution.

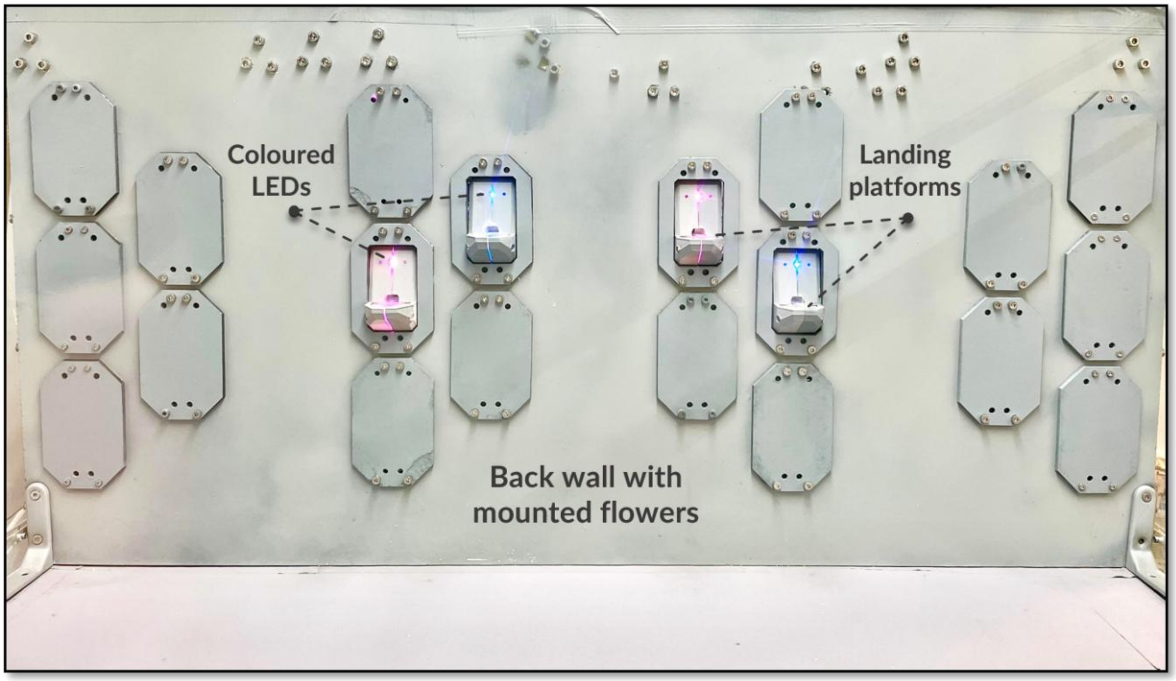

Figure 2: Back wall of the flight arena with mounted flowers. In the experiment, four flowers, two purple and two blue, were mounted and active among the 20 available flower sockets.

System specifics

Bee detection and LEDs

Each flower is equipped with a PiCamera compatible with the Raspberry Pi. Bees are individually tagged with unique ArUco markers glued on their thorax. These markers feature distinct black-and-white square patterns (see **Fig. 1**), each corresponding to a number (1–99) and enabling real-time detection.

Flowers are equipped with two RGB LEDs wired in parallel: one at the front and another below the landing platform, to maximise colour visibility to the foraging bees. The wavelength and intensity of the RGB LEDs can be adjusted for each flower, and a third, white LED inside the flower provides illumination for the camera to detect bees.

Feeder and solution delivery

Each flower contains a feeder which consists of a 3D-printed cup with a capacity of 50 µL, connected to four peristaltic pumps via 0.5 mm silicone tubing for precise liquid delivery. The pumps, concealed behind the arena wall, are driven by stepper motors to move the liquid by squeezing the tubing in a wave-like motion.

Pumps 1 and 2 dispense sucrose solutions of different concentrations or plain water, while pumps 3 and 4 handle feeder cleaning—pump 3 first rinses it with water to remove residual sucrose, and pump 4 flushes out the remaining liquid. The pumps are connected to large refillable bottles that store sucrose solutions and water, as well as collect waste from the flushing process.

Each flower can dispense two different sucrose volumes and concentrations. Depending on the experimental conditions and flower configuration, pump 1 or 2 delivers sucrose solution of either quality 1 or 2 to the feeder, with a minimum delivered volume of 6 µL.

System configuration and data

Before an experiment, a configuration file is created to define the settings for each flower, including: its colour, the volume and concentration of sucrose solution dispensed by pumps 1 and 2, and the assignment of sucrose solutions for each bee group. For example, bees in group A receive solution 1 from one flower type and solution 2 from the other, while bees in groups B and C receive the same solution from both flower types.

Each flower is also assigned a retention time, which defines the minimum interval before the same bee can receive sucrose solution from that flower again. This prevents bees from repeatedly revisiting the same flower in quick succession. Additionally, bees must exit and re-enter a flower to receive sucrose, ensuring they do not remain inside and trigger repeated scans resulting in continuous sucrose dispensing.

During an experiment, foraging data is recorded in real-time on the central hub computer, including, for each flower: (1) the bee ID entering the flower, (2) the quality and quantity of the solution dispensed, and (3) the bee ID exiting the flower—each event recorded with its corresponding timestamp. A bee is considered to have collected the solution if more than 5 seconds elapse between solution dispensing and flower exit; otherwise, the solution is classified as uncollected.

Experiment

This pilot experiment tested the foraging behaviour of bees on the robotic flower system and assessed its reliability. The experiment ran continuously for one week, from May 31 to June 7, 2023, using a single colony. Flowers were automatically activated each day at 6:00 AM and deactivated at 8:00 PM.

Four flowers were used: two blue (B1 on the left, B2 on the right) and two purple (P1 on the left, P2 on the right), positioned from the bee's perspective upon entering the arena (see **Fig. 2**). Bees that had foraged regularly on *ad libitum* artificial flowers the week before the experiment (refer to Colony setup section) were tagged with ArUco markers and randomly assigned to one of two groups:

1. **Group A** received 10 µL of high-concentration sucrose solution (40% w/w) from blue flowers, and 10 µL of low-concentration sucrose solution (15% w/w) from purple flowers;
2. **Group B** received the reverse, with the high-concentration sucrose solution from purple flowers and low-concentration solution from blue flowers.

Blue flowers used RGB (0, 0, 255) LEDs (~460–470 nm), and purple flowers used RGB (127, 0, 127) LEDs (~430–450 nm). The retention time for all flowers was set to 60 seconds, meaning each flower could dispense sucrose to the same bee once per minute.

Data analysis

We tested whether bees preferred the more profitable flower type, predicting that group A would favour blue flowers and group B would favour purple flowers. To assess this, we analysed (1) flower visits (i.e., bees scanned upon flower entry), and (2) flower collections (bees remaining at the feeder for at least 5 seconds after solution dispensing, indicating consumption).

Data processing was conducted in Python (v3.11, Python Software Foundation, 2023) using the *pandas* library (McKinney, 2010) for data structuring and *seaborn* (Waskom, 2021) and *Matplotlib* (Hunter, 2007) for data visualisation.

Preliminary Results and Discussion

One flower (B1) malfunctioned during the experiment and was turned off from June 4 to June 7 due to a pump leak. In total, only four bees foraged on the flowers: three from group B (bee IDs 58, 64, and

91) and one from group A (bee ID 25). However, the forager from group A was far less active than those from group B.

The three most active foragers (bees 58, 64, and 91) visited both low- and high-quality flowers throughout the experimental week (see **Fig. 3**). Over time, the two most active individuals (bees 58 and 64) gradually shifted toward visiting high-quality flowers more often than low-quality ones. Most visits involved sucrose collection regardless of reward quality, with the exception of bee 58, which often visited flowers without collecting nectar—particularly on June 3.

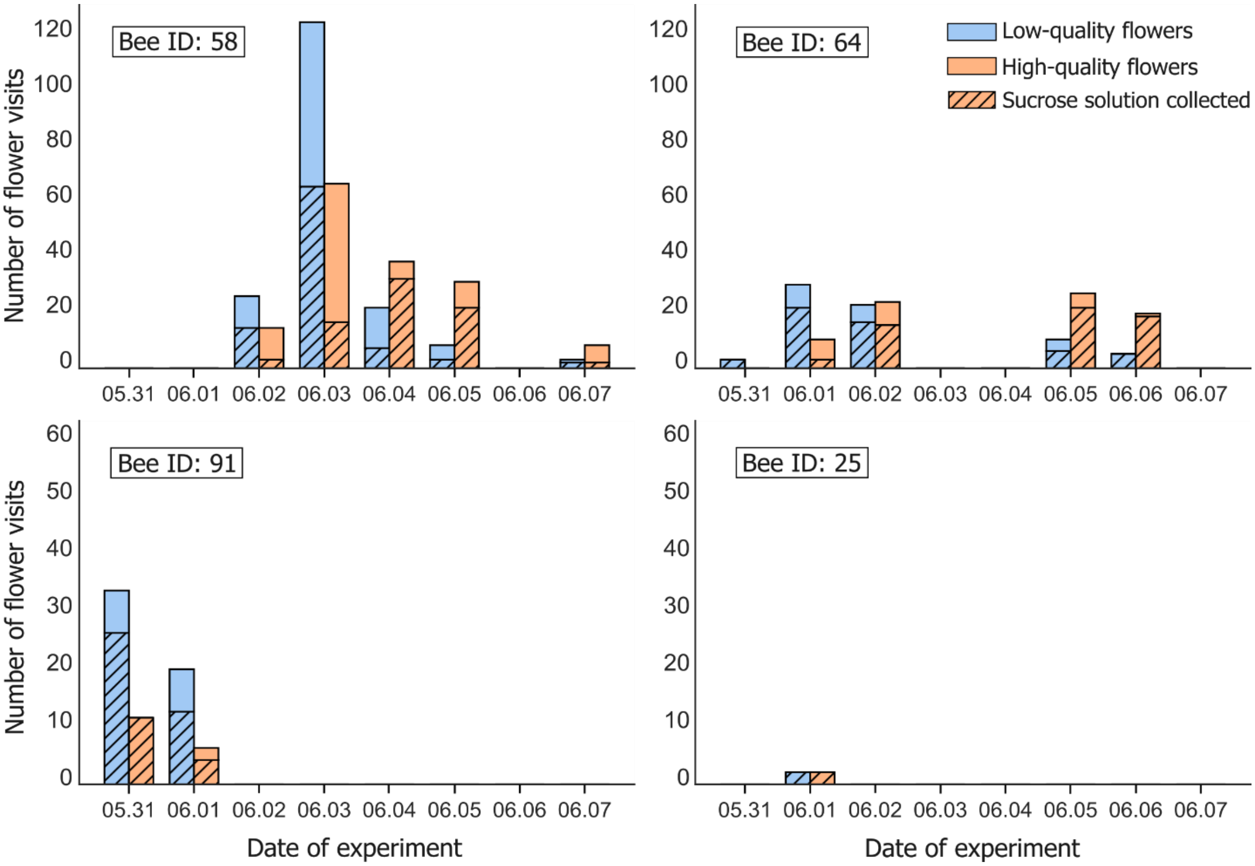

Figure 3: Flower visits and sucrose collection throughout the experiment. The first row presents the most active foragers (Bees 58 and 64), while the second row shows moderately active ones (Bees 91 and 25). Blue bar plots indicate visits to low-quality flowers (15% w/w sucrose solution), and orange bars represent visits to high-quality flowers (40% w/w). Hatched sections within the bar plots represent the number of flowers from which bees collected sucrose solution.

Only a few foragers were active during the experiment, likely due to the advanced age of the colony—over a month old at the time of testing, which is relatively old for our lab-reared colonies. The queen had already started producing males, which often signals the decline of colony activity. Although bee activity in the arena was not continuously monitored, daily observations suggested that all active foragers visited the artificial flowers at least once. Bees 58 and 64 were especially active, making several hundred visits over the course of the experiment. These preliminary results show that bumblebees can quickly learn to use the robotic flowers, consistent with other similar systems (Kuusela and Lämsä, 2016; Debeuckelaere et al., 2024).

Because all truly active foragers belonged to the same experimental group, we could not compare flower preferences across groups. Given that one flower malfunctioned during the experiment, we remain cautious in drawing ecological conclusions from the observed foraging behaviour. We tentatively suggest that bees visited both flower types because only three flowers were functioning reliably. This limited amount of sucrose available (approximately 30 µL in total, compared to a typical crop capacity of 120–180 µL in *B. terrestris* workers; Lihoreau et al., 2010), along with a one-minute refill delay and potential competition between foragers, likely encouraged bees to visit all available flowers during their foraging trips.

It also remains unclear whether bees based their flower choices on colour or spatial location. We used blue (~460–470 nm wavelengths) and purple (~430–450 nm) LED flower colours, both within the bee visual range (300–650 nm; Lunau, 1990), but their ability to discriminate between specific LED hues is uncertain. However, previous studies suggest they might. De Vries et al. (2020) examined how *B. terrestris* responded to LED colours by tracking 3D flight trajectories and found subtle changes in flight dynamics, suggesting that bees could perceive and adapt to these colours. Similarly, honeybees have been shown to distinguish between closely related LED colours using ultraviolet and blue photoreceptors (Reser et al., 2012).

This pilot experiment revealed persistent technical issues with the flower system. In particular, the peristaltic pumps, already prone to leaking before testing, failed in one flower mid-trial. The main limitation of the current design is the lack of direct monitoring inside each flower. For example, pump malfunctions can go unnoticed unless they cause visible leaks. While the inside camera can track bee visits, it cannot capture drinking behaviour or show how much solution remains in the feeder. As a result, it is unclear whether bees actually collect the solution or leave without feeding: this can only be inferred from the time they spend inside the flower, which is an uncertain proxy.

Although the hardware requires further refinement, these preliminary results highlight the software's reliability: the system ran continuously for over a week without interruption, and the flowers consistently detected bee visits, generating high-resolution behavioural data. These programmable flowers show strong potential for studying bee foraging and cognitive biases. The following sections highlight key advantages and future applications.

One of the key strengths of this system is its ability to control sucrose solution rewards, such as concentration, volume, delivery timing, or even the complete absence of reward, as well as the associated floral traits like colour and scent. These parameters can be adjusted dynamically, either over time or in response to specific foraging behaviours. This makes the system particularly well suited for testing valuation-based cognitive biases: in the case of foraging bees, how individuals perceive and assign value to different flower options.

For instance, loss aversion, the tendency to weigh losses more heavily than equivalent gains (Kahneman and Tversky, 1979), could be tested by having a flower initially offer a large volume of high-concentration sucrose solution, then flushing out the feeder content before the bee collects it fully. Even though the bee still receives some reward, the reduction may be perceived as a loss, and loss-averse individuals may then avoid these flowers, even if the collected reward matches or exceeds that of other flower options. To the best of our knowledge, loss aversion has surprisingly never been studied in bees.

Temporal discounting, the tendency to devalue rewards that are delayed in time (Frederick et al., 2002), is another evaluation-based bias that could be tested by offering bees a choice between two flower types: one offering small, immediate sucrose rewards, and another offering larger rewards after a delay, implemented through longer refill intervals. Bees that prefer the immediate but less profitable reward would thereby exhibit temporal discounting. Berby (2021) and Bjurgren (2024; master theses, non peer-reviewed) found that bumblebees preferred delayed, more concentrated sucrose rewards even despite long delays, suggesting a notable capacity for self-control. Similarly, risk aversion or risk seeking, while not classified as cognitive biases, can also lead to suboptimal decisions (e.g. Shafir et al., 1999; De Agrò et al., 2021). These could be tested by varying reward quality and frequency, to assess whether bees prefer safer options or take risks for the chance of a larger payoff, and under what conditions such preferences may shift.

Another class of testable biases includes probability fallacies, where individuals systematically misjudge likelihoods. These could be effectively tested by manipulating reward patterns over time. A well-known example is probability matching, where individuals choose options in proportion to their reward probabilities rather than consistently selecting the best option (Neimark and Shuford, 1959). For instance, if one flower type provides sucrose 80% of the time and another only 20%, a bee exhibiting probability matching would visit the two flower types in an 80:20 ratio, matching the reward probabilities instead of always choosing the 80% flower to maximise returns. MaBouDi et al. (2020) found that bees followed such a probability matching rule, selecting flower colours in proportion to how often they had been rewarded rather than consistently choosing the more reliable option. Likewise, Greggers and Menzel (1993) found bees chose feeders in proportion to their reward rates, rather than favouring the high-reward feeders.

Memory-based biases can also be tested by manipulating reward contingencies. One example is confirmation bias, the tendency to favour information that supports prior beliefs or expectations (Wason, 1960). This could be tested by first training individual bees to associate one flower colour with a high-quality sucrose reward and another with a lower-quality or absent reward. Once bees form a preference, the reward contingencies would be reversed. If bees continue to visit the originally preferred flower despite receiving repeated lower rewards, it would suggest they are relying on initial experience and ignoring new, conflicting evidence.

Another advantage of the system is that a single flower can deliver different rewards to different individuals, as shown in our pilot experiment. This feature is ideal for testing social learning biases, such as conformity bias: the tendency to adopt the behaviour of the majority, even when it conflicts with personal experience (Boyd and Richerson, 1988). For example, one bee could be rewarded for visiting one colour, while most others are rewarded for another. If the focal bee follows the majority despite receiving no reward or a lower one, it would indicate a conformity bias, where social cues override an otherwise reliable individual foraging experience. Such behaviour has been observed by Avarguès-Weber et al. (2018), where bumblebees persisted in visiting flowers occupied by conspecifics, even when these flowers offered lower rewards.

Although the manipulations enabled by this robotic system may seem artificial, the resulting experiments can nonetheless be ecologically relevant. Natural environments are highly variable (Austin et al., 2018), and floral traits like nectar quality, colour, and scent fluctuate considerably over time (Weiss, 1991; Goulson, 2003). Automated flower systems allow this variability to be simulated without human interference. This is particularly relevant when investigating judgement biases like optimism or pessimism, as they were shown to be more reliably expressed in low-stress environments (Zidar et al., 2018). Likewise, heuristics often emerge in complex, uncertain environments (Gigerenzer, 2008), and many deviations from rationality may represent adaptive responses to unpredictability (Houston et al., 2007).

Traditional behavioural studies are often constrained by small sample sizes and limited observation periods, making it difficult to detect subtle cognitive biases. By contrast, automated systems enable continuous, long-term data collection from many individuals, dramatically increasing statistical power. This is particularly valuable for detecting biases or decision rules that emerge gradually through learning, experience, or changes in internal state. Muth et al. (2018), for example, estimated that detecting subtle learning differences in bumblebees would require over 150 individuals per condition—numbers rarely feasible without automation.

Compared to existing robotic flower systems (e.g. Kuusela and Lämsä, 2016; Debeuckelaere et al., 2024), our system was designed to enable more sophisticated manipulations of perceived reward value. While previous designs are robust and effective for field studies, they are limited in their ability to deliver tailored rewards or dynamically adjust parameters at the individual level. In contrast, our system provides flexible control over reward concentration, volume, timing, and delivery itself, making it particularly well suited for investigating cognitive biases based on comparison or expectation for instance.

Nonetheless, no experimental system is without limitations, and automated flower setups come with practical challenges. Although our design is relatively low-cost and built from off-the-shelf components, assembling and maintaining multiple robotic flowers still requires basic programming and engineering skills. Technical failures can disrupt trials, potentially confusing bees and compromising data quality, and individuals may need time to accept artificial feeders. Tags glued on bees can also fall off or get dirty, making tracking unreliable. Encouragingly, in our pilot experiment, bees quickly learned to forage from the robotic flowers, and tag detection remained consistent throughout the experiment.

Animal behaviour research is increasingly being transformed by technological innovation. New tools are converging toward a common goal: enhancing the scale and precision of behavioural data while reducing human effort and error (Orbán and Plowright, 2014b). The robotic flower system presented in this study remains a prototype but shows strong potential for testing a wide range of cognitive biases: both classic biases that have not yet been tested in invertebrates, likely due to methodological constraints, and other biases already documented but now more accessible through automation. Future studies could build on the framework and ideas outlined here to develop their own systems or explore cognitive biases that remain unexplored in insects. The development of automated experimental systems is both timely and necessary, as understanding how individuals perceive and evaluate options is essential for advancing our knowledge of insect decision-making.

Supplementary Material

S1 contains video clips of bees foraging during the experiment and **S2** includes the dataset. Supplementary materials are available on Zenodo (https://doi.org/10.5281/zenodo.15131554).

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Authors Contribution

Mélissa Armand: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualization. **Massimo De Agrò:** Conceptualization, Investigation, Methodology. **Tomer J. Czaczkes:** Conceptualization, Methodology, Validation, Resources, Supervision, Project administration, Funding acquisition.

Robotic flower system: T. J. C. and M. D. A. conceptualised the system; M. D. A. designed and built the robotic flowers; M. A. made modifications and improvements to the system.

General Discussion

Foraging bees make countless flower choices over their lifetime. Like customers faced with overwhelming shelves of products in a supermarket, bees navigate complex, dynamic floral environments and must make smart decisions; but unlike most shoppers, their choices have immediate consequences for their own survival and that of the colony. It is rarely possible to evaluate every available option and its associated costs and benefits, so bees often rely on simple decision rules to guide their choices. These shortcuts, however, make them especially vulnerable to perceptual biases, just like shoppers are influenced by colourful packaging, expectations, or prior experiences, and can lead to judgement errors and suboptimal decisions. In this thesis, the flower choices of individual bumblebees (*Bombus terrestris*) were explored through the lens of value perception: we examined individual differences in foraging behaviour, tested their flower preferences across varying conditions, and investigated their sensitivity to cognitive biases. Foraging bees: *bee*-yond rational?

To understand how bees evaluate and choose flowers, we first examined individual differences in their foraging behaviour. We found that bees varied in how selective they were towards flower quality and in the trade-offs they used to optimise foraging. These differences were shaped by early experiences and environmental conditions. We then asked whether their flower choices were influenced by variability in a neutral cue, focusing on floral scent. Bees readily foraged on all flowers, showing no preference for consistent or variable scents. Building on this, we explored whether cognitive biases affected how bees perceived flower value. We tested the peak-end effect, where a disappointing final reward may reduce the perceived value of an otherwise rewarding flower option, and the decoy effect, where unrewarding flowers may increase the appeal of neighbouring flowers by contrast. Bees showed no clear peak-end effect but still did not prefer the flower with the highest total reward, likely due to an incentive contrast effect. Similarly, bees showed no decoy effect, foraging equally from rewarding flowers and quickly learning to avoid unrewarding ones.

These main findings offer new insights into how bees make flower choices, but also raise further questions, particularly about their foraging behaviour and interindividual variability, the factors that shape these behaviours, and how such factors influence value perception and decision-making. In the following sections, I explore these questions by discussing the thesis results in detail, beginning with foraging behaviour and individual differences among bees.

Foraging behaviour and individual differences

A key finding across this thesis is the remarkable speed and consistency with which bumblebees improved their foraging efficiency. Within just a few bouts, bees adapted to diverse floral environments, regardless of differences in flower types, spatial layouts, sensory cues, or reward structures. They quickly learned to avoid low-reward or unrewarded flower options (**Chapters 1**, **3**, and **4**), reduced revisits to depleted flowers (**Chapters 1**, **2**, and **4**), and made increasingly fast and accurate choices during foraging (**Chapters 1** and **4**). These improvements were especially striking in **Chapter 1**, where bees in both favourable and challenging environments reached similar sucrose intake rates after just three bouts, using distinct foraging patterns and context-specific trade-offs. Although not formally analysed, bees also increasingly developed more structured foraging patterns with each bout, including more systematic movements between flowers and patches, faster sucrose collection, quicker returns to the arena after unloading, and even anticipation of reward locations in experiments where flower types alternated sides (**Chapters 3** and **4**).

Across experiments, bees rapidly learned to handle a wide range of artificial flower types and navigate diverse floral setups. These included scent-variable and colour-diverse arrays (**Chapters 1–5**), patchily distributed resources (**Chapters 1** and **4**), and even dynamically changing flowers, swapped between visits in wall-mounted slits, requiring bees to track shifting locations (**Chapter 3**). They also adapted to a variety of flower morphologies, from umbel-shaped inflorescences to robotic flowers with concealed feeders. These results align with extensive research showing that bees adjust their foraging to maximise energy efficiency (Makino and Sakai, 2004; Lihoreau et al., 2010; Combes et al., 2020), rapidly associate sensory cues with rewards (Laverty, 1994; Kunze and Gumbert, 2001; Sherry and Strang, 2015), avoid unrewarded options after only a few encounters (Saleh and Chittka, 2006; Raine and Chittka, 2007), and handle flowers with diverse morphologies effectively (Heinrich, 1979b; Pyke, 1979; Hodges, 1981).

As outlined in the **General Introduction**, bee foraging is marked by striking interindividual variability (Saleh and Chittka, 2006; Woodgate et al., 2016; MaBouDi et al., 2020b). This variation was explored most extensively in **Chapter 1**, while the other chapters focused more on group-level foraging patterns. Nevertheless, individual differences emerged across experiments, particularly in flower choices, colour preferences, and learning abilities.

Bees varied widely in their flower choices (**Chapter 1**), both in how picky they were about sucrose quality and in the trade-offs they made between reward concentration, volume, speed, and accuracy. Remarkably, as bees gained experience, these preferences and patterns persisted over time. Similarly, Thomson et al. (1997) found that even when bees foraged in the same flower array, they visited different plants and followed distinct movement patterns. Woodgate et al. (2016) tracked four *B. terrestris* workers across their entire foraging careers and observed stable, marked differences in how they explored and exploited their environment. Likewise, bee studies have reported consistent interindividual differences in speed–accuracy trade-offs (Chittka et al., 2003; Skorupski et al.,2006; Burns and Dyer, 2008).

We also found interindividual differences in colour preferences. In **Chapters 1** and **3**, most bees preferred yellow and blue flowers, respectively, yet a notable minority favoured the alternative. In **Chapter 4**, some bees initially chose yellow flowers, likely due to colour generalisation from pre-training. In line with this, Sanderson et al. (2006) reported stable individual differences in honeybee preferences for either blue or yellow flowers, independent of handling time or reward. Beyond individual variation, we also observed colony-level differences. In **Chapter 1**, bees generally preferred yellow over blue, while in **Chapter 3**, the opposite was true. This inconsistency suggests that colour biases may vary not only across individuals, but also between colonies. Similarly, Ings et al. (2009) found both population-level (*B. terrestris audax* vs. *B. terrestris dalmatinus*) and colony-level differences in innate colour preferences.

Can interindividual differences in bee foraging behaviour be beneficial? In **Chapter 1**, bees' innate bias for yellow or blue led them to first encounter either high- or low-concentration sucrose solution, shaping their reward expectations and subsequent flower choices. Some bees became highly selective, while others remained more flexible and exploratory— different foraging styles that may be advantageous in varying settings. Supporting this, Dyer et al. (2014) identified three distinct foraging "tactics" in bees and showed, through simulations, that each conferred advantages under different conditions: some bees performed better when rewards changed frequently, while others excelled when conditions were stable. Similarly, individual variation in foraging patterns has been shown to enhance colony performance (Muller and Chittka, 2008; Burns and Dyer, 2008; Holland et al., 2021). Differences in colour preference may also be beneficial: Raine and Chittka (2007) found that bees with an innate bias toward violet flowers collected significantly more nectar than those without. Since some flower colours tend to be more rewarding in nature (Giurfa et al., 1995), such biases may provide an ecological advantage.

Factors shaping foraging behaviours

We have seen that bees displayed a wide range of foraging behaviours, with notable differences between individuals. What underlies this behavioural diversity? In this section, I explore the key factors that shaped bees' flower choices. Across experiments, their foraging was influenced by a combination of sensory cues, learning processes, environmental conditions, prior experiences, and reward quality.

The most apparent factor influencing bees' foraging behaviour was sensory cues, particularly colour. Colour preferences had a strong impact on flower choice, potentially overshadowing other effects (see Limitations and perspectives section). Across experiments, bees consistently favoured certain flower colours, even when all flowers offered equal rewards. In **Chapter 1**, most bees made their first visit to yellow flowers, likely drawn by their brightness or salience. A similar, though non-significant, trend for yellow was observed in **Chapter 2**. In contrast, blue flowers were favoured by bees in **Chapters 3** and **4**, with a particularly strong effect in **Chapter 3**, where colour influenced flower choice in a binary test more than reward sequence. These robust biases align with numerous studies showing innate colour preferences in bees, notably for blue and yellow (Lunau 1990; Giurfa et al. 1995; Raine and Chittka, 2007), and support the role of colour as a key driver of flower choice (Spaethe et al., 2001; Morawetz et al., 2013). Gumbert

(2000), for example, showed that even after training on different colours, bees' initial preference for specific wavelengths re-emerged, highlighting the persistence and strength of colour biases.

Scent, by contrast, played a minor role in flower choice, although olfactory cues were only used in a single experiment. Bees showed no preferences between overall scent bouquets or individual scents, and foraged equally from flowers with consistent or variable scent profiles (**Chapter 2**). This suggests that bees treated scent as a neutral cue signalling reward presence, rather than as a feature driving choice in itself—unlike colour. These findings contrast with previous studies showing that bees can exhibit strong innate scent preferences that influence foraging decisions (Raguso, 2008a; Majetic et al., 2009), sometimes even overriding colour cues when both are present (Gegear and Laverty, 2001; Gegear, 2005). One possible explanation is that the artificial scents used (strawberry, rose, lemon, and vanilla) lacked ecological relevance and therefore failed to elicit innate preferences.

Learning is another key driver of foraging behaviour. As discussed in the previous section, differences in learning ability likely contributed to interindividual variation in foraging. Across all chapters, bees learned to associate both colour and scent cues with rewards—and the absence thereof, which in turn guided their flower choices. Even when scent cues varied across flowers (**Chapter 2**), bees still foraged effectively, suggesting robust learning that tolerates a degree of cue variability. These findings contribute to the extensive body of research showing that bees are highly proficient at learning and remembering cue–reward associations (see review by Sherry and Strang, 2015).

However, the strength of learning appeared context-dependent. For instance, colours associated with sharply contrasting rewards, such as in the control experiments designed to test whether bees could distinguish colours (**Chapters 1**, **2**, and **3**), elicited strong learning with bees overwhelmingly choosing the higher-reward option. Similarly, in **Chapter 1**, bees foraging in a "harsh" array with only half of the flowers rewarding learned faster to prioritise the colour associated with best rewards compared to bees foraging in a more favourable array. These findings suggest that greater ecological stakes can enhance learning, likely due to increased selection pressure for efficient foraging.

Nevertheless, learned cue–reward associations did not prevent revisits to empty flowers, even when flowers differed in colour (**Chapters 1**, **3**, and **4**)—a behaviour consistent with previous findings and likely reflecting memory limitations (Chittka et al., 1999; Forster et al., 2023a). Altogether, these results highlight the importance of ecological context and task complexity in shaping learning performance. For example, Muth et al. (2015) showed that high-reward contexts boosted motivation and persistence in difficult learning tasks, while Saleh and Chittka (2006) found that individual bees converged on trapline routes at different speeds depending on environmental complexity.

Prior experiences and environmental conditions also shaped foraging behaviour. The most striking example comes from **Chapter 1**, where bees' very first flower visits had lasting effects on their pickiness for sucrose concentration, influencing subsequent flower choices and overall foraging patterns. As noted above, environmental harshness also affected how quickly and selectively bees favoured high-reward flowers. Strong initial colour biases, particularly in **Chapters 1** and **3**, sometimes dominated learned associations and continued to guide flower choices even after multiple foraging bouts. In **Chapter 4**, the colour of pre-training flowers likely influenced the first flower choice of some bees, further suggesting that early experience shaped foraging decisions. These findings align with earlier studies showing that past experiences can have lasting effects on flower preferences (Jaworski et al., 2015; Hagbery and Nieh, 2012; MaBouDi et al., 2020a). Environmental factors such as reward predictability, patch structure, and spatial layout were also shown to influence foraging patterns (Biernaskie et al., 2009; Woodgate et al., 2016; Hemingway et al., 2024a).

Sucrose rewards also influenced flower choice, but not in a straightforward or strictly optimal manner. In **Chapter 3**, bees did not prefer the flower type offering more total sucrose when the final reward was of lower quality. Similarly, in **Chapter 1**, not all bees prioritised the highest sucrose concentration or maximised the volume of solution collected: bees in the low-pickiness cluster prioritised sucrose volume over concentration, while those in the high-pickiness cluster surprisingly sacrificed reward volume for faster foraging. These patterns are consistent with previous findings that bees do not always select the most rewarding flowers (Abrol, 2006; Frasnelli et al., 2021; Nityananda and Chittka, 2021), likely reflecting the complexity of foraging environments and the subjective nature of reward evaluation (see next section).

While various factors influenced bees' foraging, they also showed flexibility in their responses to external conditions. In some cases, they adapted their behaviour; in others, they appeared to ignore these influences altogether. In **Chapter 1**, for example, bees appeared to compensate for their initial conditions and ultimately reached similar sucrose intake rates across groups, despite foraging in more or less favourable environments. Other factors, contrary to expectations, had little or no effect on behaviour. These included variability in scent, reward order, and the presence of rewardless flowers (**Chapters 2**, **3**, and **4**). In the next section, I explore how the factors shaping foraging behaviour may influence value perception and the decision-making processes underlying bee flower choices.

Value perception and decision-making

We have seen that bees displayed various foraging behaviours shaped by factors such as sensory cues, learning, prior experiences, and environmental conditions. In this section, I examine how these factors shaped how bees perceived their flower options and made foraging decisions. Across experiments, bees made context-dependent choices, exhibited incentive contrast effects, and appeared to rely on simple heuristics when selecting flowers.

In **Chapter 3**, we tested a well-known cognitive bias, the peak-end effect, and found a more nuanced outcome than expected. Contrary to our hypothesis, bees did not prefer flowers offering three consistent high-concentration sucrose drops over flowers that included an additional, lower-concentration final reward. Yet, they also did not favour this “poor-end” flower, despite it offering more total sucrose. Why not? Probably because bees did not benefit from the extra reward—simply because they did not collect it! Having previously experienced higher-concentration sucrose, the final, lower-quality drop was often rejected by bees. This response reflects a negative incentive contrast effect, a well documented phenomenon in foraging bees where individuals often reject downshifted rewards after previously encountering higher-quality ones (Bitterman, 1976; Waldron et al., 2005; Townsend-Mehler et al., 2011).

As seen in the previous section, prior experiences shaped bee behaviour; incentive contrast effects arise precisely from valuing rewards relative to those encountered previously. In **Chapter 1**, a similar pattern emerged: the concentration of the first sucrose reward collected influenced bees’ subsequent acceptance or rejection of low-concentration rewards. Bees that initially experienced high-concentration sucrose were more likely to reject lower-quality flower options later on. This suggests another instance of negative incentive contrast, where perceived value, rather than absolute reward, shaped preferences and flower choices.

In fact, bees appeared to rely on internal thresholds of minimal acceptable sucrose concentration, below which they did not collect the reward. In **Chapter 3**, most bees were observed probing the final low-concentration drop and then leaving it uncollected. Similarly, in **Chapter 1**, this threshold was especially evident in high-pickiness bees, which continued to visit low-quality flowers (likely due to memory constraints and the patchy distribution of alternating good and poor flowers) but consistently rejected those rewards after probing. These patterns suggest that bees evaluated rewards against internal expectations shaped by prior experience. Such acceptance thresholds resemble a simple “if/then” heuristic (Gigerenzer and Todd, 1999): “if sucrose concentration exceeds a certain threshold, collect; otherwise, reject”. Previous studies have described a similar threshold departure rule, where foraging bees left a plant after probing a flower whose nectar volume was below a certain level (Pyke, 1982; Hodges, 1985).

Likewise, the foraging trade-offs observed in **Chapter 1** may reflect the use of simple heuristics: bees consistently prioritised certain features, such as sucrose concentration or foraging speed, over others. This suggests they may have relied on limited information when making decisions, rather than evaluating all available options. For example, high-pickiness bees almost always rejected low-reward flowers even after landing on them, while low-pickiness bees collected low-quality rewards despite better ones being available. While these choices led to efficient foraging, they were not strictly optimal. However, these behaviours could also result from reinforcement-based learning rather than fixed heuristics, and it is unclear which process drove the observed patterns.

In **Chapter 4**, bees did not display a decoy effect: the presence of unrewarded “decoy” flowers within a patch did not make them favour nearby rewarding flowers, contrary to expectations. Likewise, probing a rewardless flower in one bout did not increase the likelihood of revisiting the same inflorescence in the next. Like the peak-end effect, the decoy effect is thought to result from comparison-based processing, where rewards are judged not in isolation but relative to other available or recently experienced options. In **Chapters 1** and **3**, bees appeared to compare current rewards with those previously collected, yet no similar contrast-based effect emerged in **Chapter 4**. One possibility is that the complete absence of sucrose in decoy flowers made them clearly irrelevant, prompting bees to disregard them rather than include them in internal comparisons. As a result, the decoys had no apparent influence on the perceived value of nearby rewarding flowers.

Many of the foraging decisions discussed earlier appear to be context-dependent. For example, bees' foraging patterns and sucrose selectivity shifted with environmental conditions (**Chapter 1**); sucrose solution accepted as baseline food in the nest (20% w/w) was later rejected when offered as a lower-quality reward (**Chapter 3**); and low-quality options influenced flower choices in some contexts (**Chapters 1** and **3**) but not in others (**Chapter 4**). Bees also responded differently to variability depending on context: scent variability had no effect on flower choice (**Chapter 2**), whereas variability in reward quality did (**Chapters 1** and **3**). Similarly, previous studies have shown that bees may reject rewards they previously accepted if they had experienced better ones beforehand (Bitterman, 1976; Wiegmann et al., 2003; Townsend-Mehler et al., 2011). Together, these findings suggest that bees' valuation processes are highly context-sensitive.

Across experiments, we have seen that bees made foraging choices based on the relative value they assigned to different options. But did these choices reflect irrational or suboptimal decisions? For example, bees did not prefer the peak-end sequence, even though it offered more total reward. Since most bees did not actually collect the extra sucrose, their choice could be seen as economically rational, i.e., coherent with their internal logic (Kacelnik, 2006). From an ecological perspective, however, it was suboptimal, as they missed a chance to collect more nectar. Conversely, context-driven shifts in foraging behaviour may have been ecologically beneficial, yet still violated the principle of regularity—a key concept in rational choice theory, which states that preferences should remain stable across contexts (Huber et al., 1982; Tversky and Simonson, 1993). In the next sections, I consider the broader implications of such deviations from rational choice, beginning with their consequences for bee fitness.

Implications of biased value perception for bee fitness

We have seen that bees' foraging behaviour was shaped by external cues, learning, and environmental context, and that their flower choices depended on how they perceived the value of each option. This value perception was highly context-sensitive, notably shaped by prior foraging experiences and by the other flower options in the choice set. Our results highlight the bounded rationality of bees (Simon, 1955): individuals relied on simplified decision rules shaped by cognitive and environmental constraints, often deviating from strict economic rationality. In this section, I explore the fitness consequences of bees' deviations from rationality, particularly in relation to their foraging efficiency and flower choices.

Our findings align with empirical research in animal behaviour showing that individuals are not perfectly rational agents who evaluate all available options and consistently choose the one with the highest expected utility (Shafir, 1994b; McNamara et al., 2006; Trimmer et al., 2011). In real-world situations, decision-making is constrained by time, energy, and context (Houston and McNamara, 1981), and individuals often rely on a mix of intuitive and analytic reasoning (Evans, 2008). They frequently use heuristics and attend to only a subset of available information, which can result in seemingly irrational choices. Individuals are also prone to systematic distortions in value perception (cognitive biases) which can further contribute to suboptimal decisions (Tversky and Kahneman, 1974).

Although these decision-making processes remain underexplored in insects, early models of optimal foraging already used concepts close to heuristics, such as "simple foraging strategies" and "less-than-optimal models", to explain observed behaviours (Anderson, 1983). Marsh (2002) argued that studying heuristics may help explain behavioural irregularities, and similarly, Watzek and Brosnan (2021) suggested that deviations from expected value maximisation can reveal the mechanisms underlying animal decision-making. Throughout this thesis, I have highlighted numerous examples of deviations from rational choice in insects, particularly in foraging bees (see **Tables 2** and **3**, **General Introduction**), including our own experimental findings. It is now clear that bees can rely on simple heuristics and sometimes make irrational choices, and that studying such processes may advance our understanding of their flower choices. The question is how to interpret these decision-making processes; are they limitations that reduce fitness, or adaptive responses to ecological constraints? Here, fitness refers to how effectively bees collect resources to support their survival and reproductive success.

This question echoes a long-standing debate in human psychology between two opposing schools of thought. Kahneman and Tversky viewed heuristics as sources of systematic error, with cognitive biases reflecting limitations in reasoning. In contrast, Gigerenzer argued that these apparent flaws are actually adaptive, efficient solutions for real-world decision-making (Vranas, 2000).

An evolutionary perspective often interprets cognitive biases as adaptive solutions shaped by ancestral survival pressures (Haselton et al., 2009). For example, loss aversion may have evolved to protect critical resources (Kahneman and Tversky, 1984). Apparent violations of rationality, such as pessimism, contrast effects, and state-dependent valuations, are considered optimal in unpredictable or resource-limited environments, where internal states or past experiences provide useful cues (Fawcett et al., 2014; McNamara et al., 2011; Trimmer, 2013). Similarly, Ayton (2000) argued that many heuristics and cognitive biases are not signs of irrationality, but instead reflect ecologically rational strategies that support efficient decision-making, even when they violate normative rules.

Bumblebees navigate complex and unpredictable floral environments with limited short-term memory and high energy demands (Redmond and Plowright, 1996; Chittka et al., 1999; Goulson, 2010), making them ideal candidates for relying on simple decision rules. As reviewed in **Table 2**, many such heuristics, though seemingly non-optimal, clearly enhanced bee fitness by supporting efficient foraging, for instance by copying conspecifics (Smolla et al., 2016; Romero-González et al., 2020) or following stereotyped visitation patterns (Corbet et al., 1981; Harder et al., 2004). Our own results align with this: bees rapidly improved foraging efficiency, likely by applying simple rules such as accepting rewards above internal thresholds and prioritising specific flower traits.

Similarly, most cognitive biases and deviations from rationality in foraging bee studies (see **Table 3**) were not viewed as simple errors, but instead interpreted by their authors as potentially adaptive. To list just a few: honeybees that showed pessimism after being shaken were seen as exhibiting a defensive response to perceived danger, such as predation, rather than merely missing a reward opportunity (Bateson et al., 2011). In complex flower arrays, bumblebees that stuck to a single, moderately rewarding flower type, a choice that might seem suboptimal, were thought to reduce decision costs and enhance foraging efficiency (Austin et al., 2018). Likewise, bees that used probability matching, i.e., choosing flower colours based on past reward frequency rather than always selecting the best option, were thought to lower cognitive load and gain an advantage by avoiding constant comparisons under uncertainty (MaBouDi et al., 2020). Bees that preferred the most recently learned flower, even when it was less rewarding, were seen as prioritising the most up-to-date information—an adaptive strategy in dynamic floral environments where conditions can change rapidly (Nityananda and Chittka, 2021).

While ecological explanations for seemingly irrational behaviours can be compelling, not all behaviours are necessarily adaptive, and there is a risk of over-rationalising. As shown in **Table 3**, some foraging behaviours appeared clearly suboptimal, likely arising from cognitive limitations, biases, or simple errors. Heuristics, too, can lead to maladaptive choices, and several of the biases reviewed were linked to heuristic-based decision-making. Sen (1977) famously argued that any choice can be justified as utility-maximising, and unless utility is clearly defined in advance, rationality becomes difficult to disprove (Kacelnik, 2006). Although these critiques were originally aimed at economic models, the same issue applies in behavioural ecology: if every choice can be retrospectively justified as fitness-enhancing, the concept of rationality ceases to be meaningful. Rationality in animal behaviour needs to be clearly defined and empirically testable, not simply assumed (see Limitations and perspectives section).

Ultimately, deviations from rational choice can reflect both cognitive limitations and adaptive solutions. Whether a choice appears suboptimal or beneficial often depends on context—and on perspective. A behaviour that seems irrational in the lab may, for example, prove effective in natural settings (Thuijsman et al., 1995; Haselton et al., 2009; Fawcett et al., 2014). Evans (2008) argued that intuitive (fast, automatic) and analytic (slow, deliberate) processes are not inherently opposed, but represent complementary routes to decision-making. Similarly, Arkes (1991) suggested that judgement errors may not be dysfunctions, but acceptable costs of cognitive systems designed for speed and efficiency rather than perfection. From this perspective, suboptimal foraging decisions may reflect adaptive compromises, supporting bees' fitness by helping them save time and energy, or by allowing them to focus attention on more ecologically relevant cues.

Implications for plant-pollinator co-evolution

Bees' departures from rationality reflect a mix of cognitive constraints and adaptive shortcuts that bias how they perceive the value of different flower options. Because bees and flowering plants are mutualists, exchanging nectar for pollination, bees' value perception and resulting flower choices directly influence plant reproductive success. In this section, I explore how bee decision-making, particularly biased value perception, may shape this co-evolutionary relationship.

Numerous flowering plants rely on pollination services provided by insects, offering nectar and pollen in return, but it is in the plant's interest to minimise these costs while still securing effective pollination (Bronstein et al., 2006). Accordingly, plants have evolved a variety of strategies to manipulate pollinator behaviour (Shafir et al., 2003; Schaefer and Ruxton, 2009), including the use of psychoactive nectar compounds (Couvillon et al., 2015; Baracchi et al., 2017a) and deceptive signalling, such as mimicking rewarding flowers without offering a reward (Dafni, 1984). This raises the question of whether bees' distortions in value perception could similarly be exploited by plants to enhance the appeal of their flowers. Floral traits often seen as honest signals or cues for mutualistic cooperation may, in some cases, function instead as features shaped by selection to exploit pollinators' cognitive biases. The experiments presented in **Chapters 3** and **4** were designed with these ecological questions in mind, testing whether specific cognitive biases could be leveraged by plants to influence bee foraging decisions.

In **Chapter 3**, we tested whether the sequential order of nectar rewards, similar to those found in vertical inflorescences naturally foraged by bees from bottom to top (Waddington and Heinrich, 1979; Best and Bierzychudek, 1982), could elicit peak-end effects in bumblebees. We hypothesised that ending with a less rewarding flower might lower the perceived value of the whole inflorescence. This would suggest that plants could take advantage of this bias by concentrating rewards in the top flowers to make the inflorescence seem more rewarding. Although bees did not show a clear peak-end effect, their lack of preference for a flower with a greater total reward but a disappointing ending suggests that nectar distribution might still influence bee flower choice. However, earlier studies found that bees' stereotyped bottom-to-top visitation patterns remained unchanged even when reward order was reversed (Waddington and Heinrich, 1979; Corbet et al., 1981). These findings suggest that nectar distribution alone may have limited influence on bee behaviour via biased value perception.

In **Chapter 4**, we tested whether unrewarded flowers, commonly found in many flowering plants, could influence bee preferences through decoy-like effects. Some plants retain old, nectarless flowers alongside rewarding ones, and we hypothesised that these irrelevant flowers could enhance the perceived value of nearby flowers by contrast, potentially increasing pollinator visits without additional nectar investment. However, we found no evidence that rewardless flowers induced a decoy effect in bees, nor have previous studies (Shafir et al., 2002; Tan et al., 2014; Forster et al., 2023a, 2023b, 2025; Hemingway et al., 2024). Nonetheless, bees rapidly learned to avoid unrewarded flowers, potentially prompting individuals to leave an inflorescence earlier when such flowers are numerous (Biernaskie et al., 2002; Ishii et al., 2008). This could benefit plants by reducing self-pollination between flowers of the same plant (de Jong et al., 1993; Biernaskie et al., 2002). Our results suggest that while nectarless flowers do not seem to exploit pollinator biases, their presence may still serve a functional role in promoting cross-pollination.

In the literature, some findings suggest that bees' biased value perception could benefit plants. Kikuchi and Dornhaus (2018) found that bumblebees more readily learned to associate blue with rewards than to avoid it when paired with punishment—a form of asymmetric learning. The authors suggested that blue flowers may still attract pollinators even when they are imperfect mimics or lack rewards, potentially benefiting deceptive plants. Recency effects, often seen in bees and possibly driven by weak short-term memory (Redmond and Plowright, 1996), show that flower choices are strongly influenced by the most recent reward experience, even when it is lower than that of alternative options (Schmid-Hempel, 1986; Prabhu and Cheng, 2008; Nityananda and Chittka, 2021). This may benefit plants by allowing even moderately rewarding flowers to be revisited if they happen to be the last encountered on a foraging trip.

Beyond the effects of bees' cognitive biases on plant success, our experimental findings also highlight broader implications for plant–pollinator interactions and the evolution of floral traits. In **Chapter 2**, the absence of a preference for consistent versus variable scents suggests that plants may not be under strong selection to maintain tightly controlled scent profiles across flowers. When rewards are equal, scent uniformity alone may not influence flower choice. This apparent lack of selection pressure may help explain the high intraspecific variation in floral scent observed in many species (Burdon et al., 2015; Delle-Vedove et al., 2017). In contrast, olfactory traits that actively attract bees, such as scent composition or intensity (Majetic et al., 2009; Pichersky and Raguso, 2018), may be under stronger selection.

Additionally, bees' sensitivity to negative incentive contrasts and internal acceptance thresholds (**Chapters 1** and **3**) suggests that sudden drops in nectar concentration can prompt them to abandon flower patches prematurely, consistent with previous findings (Cresswell, 1990; Keasar et al., 2002; Biernaskie et al., 2002). This implies that plants may benefit from avoiding especially poor rewards, as these can deter continued visitation (but see potential benefits for cross-pollination above). Across our experiments, visual cues, particularly certain flower colours and high saliency, also emerged as important drivers of flower choice (**Chapters 1**–**4**), reinforcing the established role of colour constancy in foraging bees (Heinrich, 1979; Dyer et al., 2014).

Limitations and perspectives

This thesis provided valuable insights into flower choices and cognitive biases in bumblebees. Yet, most experiments were characterised by negative results, meaning that the outcomes did not support our original hypotheses (**Chapters 2**, **3**, and **4**). While such findings are informative in their own right, they also point to limitations in experimental design that may have hindered the detection of certain effects. Reflecting on these limitations helps contextualise the results and suggests useful directions for future experiments.

A major limitation was the influence of colour biases on flower choices. Nearly all experiments were affected by bees' strong and sometimes unexpected preferences for certain colours, which influenced initial flower visits, drove flower preferences in binary tests, or contributed to borderline effects (**Chapters 1**, **3**, and **4**). Colours were used as seemingly neutral cues, easily implemented in the lab using paint or coloured materials, and intended to help bees associate specific flowers with rewards. Instead, bees treated colour as a salient feature, driving choice independently and likely masking some of the subtle effects we had hoped to detect. In hindsight, I underestimated the strength and consistency of colour biases in bumblebees. A possible solution for future experiments is to rely more on scent cues as neutral alternatives, since bees showed no strong innate preferences for any particular scent in our experiment (**Chapter 2**).

Sample sizes may have been a limiting factor as well. Although we usually tested more bees than is typical in similar studies, the number of individuals was limited by the nature of the experiments themselves. Free-flying behavioural tests were time-consuming and labour-intensive, as each bee was tested individually through multiple foraging bouts. Foraging motivation also varied unpredictably from day to day, and colony development was sometimes disrupted; queens occasionally died, ending experiments early, or produced males too soon, often reducing foraging activity. These constraints made it difficult to test large numbers of bees. In hindsight, conducting formal power analyses before the experiments would likely have helped clarify how many individuals were needed to detect subtle effects and interpret the results more confidently.

Another consideration is the structure of the experiments themselves. In all cases, a final binary choice between flower types was used as a proxy for bees' preference. While this approach provided a clear and controlled measure, a single choice may not fully capture more nuanced or dynamic aspects of decision-making. Additionally, although necessary for learning, the training bouts in which flower types were presented in alternation (**Chapters 2** and **3**) did not provide any information about preference, as bees had no opportunity to choose between options. Nevertheless, control experiments confirmed that binary choice tests were a reliable proxy for preference when flower types differed clearly in reward value (**Chapters 1**,

2, and **3**). In **Chapter 1**, binary choice proportions also aligned with group-level foraging preferences observed during training bouts where both flower types were available simultaneously.

However, this approach may also have oversimplified flower preferences, particularly in the presence of strong colour biases. For example, in **Chapter 3**, had we measured only first choices in the binary test, we would have missed the slight preference for the consistent reward sequence that emerged over repeated visits. This was not the case in **Chapter 2**, where first and consecutive choices were similar. In the cognitive bias experiments (**Chapters 3** and **4**), the binary choice test alone may have overlooked subtle effects: in both cases, small, non-significant differences in choice patterns suggested the possibility of emerging preferences, but these trends were too weak to support firm conclusions.

To address many of the limitations described above, the robotic flower system introduced in **Chapter 5** offers a promising alternative. Although still a prototype, its ability to continuously track individual bees reduces the need for labour-intensive manual testing, enables long-term experiments, and allows much larger sample sizes. The system also generates rich behavioural data over time, providing a more detailed and dynamic picture of foraging decisions. For testing cognitive biases in particular, this setup could support more complex and naturalistic foraging conditions while reducing handling stress, both factors that are known to influence the expression of heuristics and biases in animals (Gigerenzer, 2008; Zidar et al., 2018).

A promising future direction in studying cognitive biases is the exploration of emotion-like states in insects. In animal welfare research, judgement bias tasks, where individuals respond differently to ambiguous cues depending on their internal state, are increasingly used as indicators of affect or emotion (Paul et al., 2005; Mendl et al., 2009; Kremer et al., 2021). These biases are known to influence how animals process information and make decisions (d'Ettorre et al., 2017). While still debated, there is growing evidence that insects may also exhibit emotion-like responses (e.g. Yang et al., 2013; Gibson et al., 2015; Solvi et al., 2016; Perry et al., 2017). Cognitive bias paradigms may therefore offer a practical tool for investigating such internal states, deepening our understanding of insect decision-making and the broader question of whether, and to what extent, insects may experience emotion-like states (Perry and Baciadonna, 2017; Nematipour et al., 2022).

As shown throughout this thesis, the framework of rationality in animal behaviour is in need of reform. Notably, there is no consensus on whether certain observed behaviours should be classified as cognitive biases, heuristics, or something else entirely (Ellis, 2018). These interpretations remain largely subjective, especially in animal behaviour research, where concepts from behavioural economics are not yet widely integrated. For instance, only a subset of the heuristics and cognitive biases identified in review **Tables 2** and **3** were explicitly defined as such by the authors, highlighting the lack of conceptual clarity in the field.

As a result, some decision-making processes in insects remain ambiguous and difficult to categorise. For example, the Weber–Fechner law describes how perceived changes in stimulus intensity follow a logarithmic scale, making small differences more noticeable at low intensities than at high ones (Fechner, 1860). Although typically considered a sensory constraint, this phenomenon, well documented in insects, also fits the definition of a cognitive bias: it involves a biased, nonlinear perception of reward size, which can lead individuals to undervalue larger rewards and make suboptimal choices (e.g. Waddington and Gottlieb, 1990; Chittka, 2009; De Agrò et al., 2021). Similarly, peak-shifts, where individuals develop a preference for stimuli more distinct from a punished one than the originally rewarded stimulus, are usually seen as learning phenomena. Yet, they too result in predictable shifts in preference that can lead to irrational decisions. For example, Andrew et al. (2014) found that honeybees preferred a novel odour more distinct from a punished scent, even though it had never been rewarded. Lynn et al. (2005) showed that bumblebees favoured novel flower colours more different from punished mimics, even over previously rewarded flowers. These cases highlight the need for clearer conceptual boundaries of decision-making processes in insect behaviour.

Conclusion

In this thesis, I explored how individual bumblebees make flower choices, and whether their decisions can be influenced by cognitive biases that distort perception and lead to seemingly irrational choices. I hypothesised that bees may rely on simple heuristics to navigate complex floral environments, and that these shortcuts could make them vulnerable to such biases. Drawing on insights from behavioural economics, I expected bee foraging to reflect not only learning and sensory cues, but also context-dependent valuation. Across experiments, we found that flower choices were shaped by how bees perceived the value of their options. This perception was highly context-dependent, influenced in particular by prior experience and the set of flower options available at the time of choice.

Although many results contradicted our initial predictions, this thesis introduced several important firsts. It presents the first test of the peak-end effect in bumblebees, the first study to examine their responses to scent variability across flowers, and the first comprehensive review of heuristics and cognitive biases in foraging bees. Together, these contributions offer new perspectives on how bumblebees evaluate and choose between flowers, and deepen our understanding of the cognitive processes that shape their decisions.

Bumblebees are declining worldwide (Williams and Osborne, 2009; Goulson et al., 2015), and bee-pollinated crops contribute to nearly one-third of the human dietary supply (Khalifa et al., 2021). Studying their foraging behaviour is both timely and essential for supporting their conservation. Incorporating concepts like value perception, heuristics, and cognitive biases can shed light on how bees make decisions in complex environments (Marsh, 2002). More broadly, future studies in insect behaviour would benefit from considering these decision-making processes, particularly in flower-visiting insects, whose choices rarely rely on exhaustive evaluation but instead follow simpler, fallible rules.

In a visual discrimination task, Eckstein et al. (2013) showed that honeybees, monkeys, and humans used spatial cues to guide their decisions, but their performance was systematically suboptimal and all used the cues less effectively than an ideal Bayesian observer. This example illustrates that deviations from rational decision-making are not simply a matter of brain size or cognitive sophistication (Gigerenzer, 2008). In fact, many biases arise from basic perceptual mechanisms and are resistant to learning. Comparative psychology reminds us that the same illusions and tricks can fool minds across species. Biases are not anomalies; they are the norm. Cognitive biases have been documented even in unicellular organisms (Latty and Beekman, 2011), and, more recently, in artificial intelligence models (Caliskan et al., 2017).

Ultimately, the fact that foraging bees can deviate from rationality... is fascinating! Like higher-order animals, individual bees cannot take every parameter into consideration and sometimes make biased judgements and suboptimal choices. Maybe it is time to see insects as more than just utility-maximising automatons. This thesis illustrates that foraging bees make flower choices using rules of thumb, shaped by value perception, internal states, and context, and that these can lead to errors: sometimes adaptive, sometimes not. So, bumblebees: bee-yond rational? In my *bumble* opinion, yes! Like all of us. And I think that’s great news.

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