



## Trading off short-term costs for long-term gains: how do bumblebees decide to learn morphologically complex flowers?



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Many animals learn skills that can take a long time to acquire. Such learned skills may have high payoffs eventually, but during the period of learning their net profitability is low. When there are other options available, it is not clear how animals decide to learn how to perform tasks that initially have low or no benefits. Bees in particular visit many types of flowers that vary in the time required to learn how to access their food rewards. We used bumblebees (*Bombus impatiens*) to address how individuals decide to persevere with learning to handle 'complex' flowers. We tested two hypotheses: (1) individuals have unlearned preferences for more complex flowers; (2) individuals use the absolute reward value of the flower to decide whether to learn to handle a particular flower type. We presented individual bees with mixed arrays of colour-distinct 'simple' and 'complex' flowers, either containing the same value of reward, or where the complex flowers contained twice the concentration of sucrose as the simple flowers. Foragers did not show any unlearned preferences towards the complex flowers, but instead preferred the simple flowers. The strongest initial preferences were for flower colour (purple over pink). Our second hypothesis was supported, because when the purple complex flowers contained a higher reward than the simple flowers, more bees persevered with visiting them, foraging on them exclusively by the end of the test period. There was significant variation between individuals in whether they learned to handle, and how much they visited, complex flowers. These results highlight the complex interplay between unlearned biases and environmental feedback in making decisions about what to learn.

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Much learned behaviour in animals is not initially beneficial to the animal as it learns it, but instead benefits the individual in the long run. This is particularly evident in foraging behaviour. Animals may spend numerous attempts refining foraging techniques that may only be beneficial once the forager has learned how to extract the food in question effectively, so that the cost of the time invested in accessing the food is smaller than the benefit gained. For example, capuchin monkeys, *Cebus paella*, can take years to perfect their ability to crack nuts open (Fragaszy & Adams-Curtis, 1997). These animals likely suffer a cost in foraging efficiency, at least at first. Bumblebee foraging is another notable example of this. When flowers require the same amount of time to handle but differ in nectar rewards associated with a floral feature, bumblebees can rapidly learn to visit the most highly rewarding flower (e.g. Cnaani et al., 2006). However, in other cases, bumblebee individuals visit flowers that may contain high rewards but yield low initial rates of

net energy gain due to the many trials needed to learn how to access nectar efficiently (Laverty, 1980, 1994). Bumblebee foragers will sometimes persevere with learning to handle such flowers even when there are other flowers nearby containing higher net rewards (i.e. immediate rewards of lower-quality that do not require learning; Heinrich, 1979).

In the examples above, even though learning pays in the long term, it is not always clear what mechanisms influence the decision to persevere with learning a task in the short term when a more immediately rewarding option is available. In short, how does an animal decide to choose a more 'difficult' option if there is a simpler one available? One possibility for how animals might persevere with learning a task that is not immediately profitable is that there is an unlearned tendency for them to do so. This would mean that a particular behavioural strategy had been favoured by natural selection and that consequently the animal carries out the respective behaviour even if it is costly in the short term, as it pays in the long term. This is the case for many learned behaviours that do not become efficient until the individual reaches a certain level of proficiency or until it is of a particular age. For example, play behaviour

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in mammals and some species of birds is costly and yields no immediate tangible reward, however it improves future adult motor skills and thus presumably pays in the long term (Caro, 1988). Other examples include the development of song in birds (Catchpole & Slater, 2008) and certain courtship rituals (Diamond, 1986). Alternatively, animals might not have unlearned preferences to perform a particular task, but instead use feedback from the task to determine whether it is worth persevering with it. This could be either through assessing the absolute value of the reward, the net value once handling costs have been accounted for, or via an estimation of how long it will take them to learn to perform the task effectively.

As generalists, bumblebees (*Bombus* spp.) sample many different species of flower that differ in structure and in the amount of learning that is required to extract their nectar, before specializing on one or a few types (Chittka, Thomson, & Waser, 1999). Bumblebees forage not only for themselves but also for their colony, and individuals may make thousands of flower visits per day (Goulson, 2003). This means that a slight increase in the amount of handling time per flower might incur a large time penalty overall. Thus it is important that individuals specialize on the type of flower that yields the most reward per time spent to handle it. Learning to handle a structurally complex flower is costly both in terms of the time invested and because it can interfere with learning how to handle another flower of a different morphology (Chittka & Thomson, 1997; Gegear & Laverty, 1995). This means that it is important for the forager to make the 'correct' choice in deciding which flowers to learn to handle.

The morphology of wild flowers has generally been defined in terms of how structurally 'complex' the flower is (Heinrich, 1976, 1979; Laverty, 1980). This morphological 'complexity' of a flower can be a somewhat subjective description: 'complex' flowers have a closed corolla with the nectar either concealed or in an unusual location, and they often possess bilateral symmetry such as the flower *Chelone glabra*, but can also be radially symmetrical, as in the case of flowers in the genus *Aquilegia*. 'Simple' flowers are usually radially symmetrical with an open corolla, and their nectar may be detectable to insects that land on them through sight or smell (Heinrich, 1979; Laverty, 1980, 1994), for example, *Taraxacum officinale* flowers. However, as these are rather human-subjective definitions of complexity, from the pollinator's perspective, floral complexity can be described as how long it takes an individual to learn how to effectively extract nectar from the flower. 'Simple' flowers require little or no learning according to this working definition, and 'complex' flowers require more learning (Laverty, 1994). As there may be variation between forager species in the amount of learning required to effectively handle a given flower species, how 'simple' or 'complex' a flower is will depend on the species of forager in question. However, in the majority of cases the amount of learning required to extract nectar from a flower directly relates to the more subjective view of how 'complex' the flower structure appears (Heinrich, 1979; Laverty, 1980, 1994). Note that in this paper 'complex' always refers to the complexity of handling behaviours required, not to the stimulus complexity, such as whether the floral signal belongs to multiple modalities (Leonard, Dornhaus, & Papaj, 2011).

Both field and laboratory studies demonstrate costs of extracting a nectar reward from structurally complex flowers, including increased handling time (Macior, 1966; Ohashi, 2002), making more errors (Laverty, 1980) and often failing to gain any reward during the earlier visits (Heinrich, 1979; Laverty, 1980, 1994). In a controlled field study by Heinrich (1979), inexperienced *Bombus vagans* bumblebees had 100% success at accessing nectar from simple flowers with open inflorescences (*Aster novae-angliae* and *Solidago* sp.). Their initial success on the more complex species of jewelweed, *Impatiens biflora*, was around 45%, improving to 90% only after 60

visits to that flower type. Despite this, most bees became constant to the complex jewelweed that required the most learning but had the highest nectar reward (measured as sugar per flower; Heinrich, 1979). Similarly, individuals of *Bombus* species tested on natural flowers manipulated simple flowers effectively from their first visit, whereas they took 60–100 visits to reach 90% accuracy at handling the complex flowers *Impatiens biflora* and *Chelone glabra* (Laverty, 1980). In another study, four species of naïve bumblebees (*Bombus fervidus*, *Bombus impatiens*, *Bombus rufocinctus* and *Bombus vagans*) had 100% initial success on simple flowers, but only 29–45% success on complex flowers, taking 30–60 visits to reach the level of experienced bees (Laverty, 1994). From the flower's perspective, complexity may be advantageous as it can result in specialist foragers, increasing the likelihood of the insect forager visiting the same species of flower successively and thus pollinating effectively. Because floral complexity thus leads to a small proportion of specialist pollinators being able to access the nectar reward, this selects for higher nectar production rates compared to simple flowers (Cohen & Shmida, 1993; Heinrich, 1979; Peleg, Shmida, & Ellner, 1992; Potts et al., 2003; Warren & Diaz, 2001). Therefore, the payoff for bees that learn how to effectively handle these flowers is predicted to be greater in the long term. Individuals that learn to handle complex flowers may also benefit through reduced intra- and interspecific competition (Chittka et al., 1999; Heinrich, 1979; Stout, Allen, & Goulson, 1998). While there are clear advantages then to persevering with learning how to handle complex flowers in the long term, it is not clear how individual bees decide to persist with learning them in the short term.

Here we investigate when and how *B. impatiens* bumblebees persevere with learning how to handle a flower that is morphologically complex when there is a simpler option available. Specifically we ask (1) whether individuals have unlearned biases that lead them to forage on the more complex option in spite of initial low rewards. We also ask (2) whether bees make their foraging decisions based on the reward value (i.e. nectar concentration), despite a high cost of handling. To address these two questions, we presented bumblebee foragers with arrays of artificial flowers that were either 'simple' or 'complex' and that contained sucrose solution as a reward. Both types of flowers were radially symmetrical, but the simple flowers had the sucrose solution visible to the bee upon or even prior to landing, whereas the complex flowers had the nectar hidden inside them. Thus the bees were required to learn how to access the reward in the complex flowers, which involved pushing open the petals, crawling inside the corolla and locating the sucrose solution inside. In one treatment, the two types of artificial flowers contained identical rewards, whereas in the other, the sucrose reward in the complex flowers was twice as concentrated as in the simple flowers. Bees were able to distinguish the two types of flower by colour. Hypothesis (1), an unlearned predisposition to visit complex flowers, predicts initial preferences for the artificial complex flowers over the simple flowers. Hypothesis (2), that bees use reward value as an estimate of future profitability, predicts that bees offered flowers with equal rewards should specialize on the simple flowers. On the other hand, individuals that forage on complex flowers that contain twice the reward of the simple flower should invest in learning how to access the nectar effectively from this flower type, as its eventual profitability should be higher than that of simple flowers, even if this is not the case initially.

## METHODS

### *Subjects and Maintenance*

We obtained five colonies of *B. impatiens* from Koppert Biological Systems (Howell, MI, U.S.A.) and marked all bees using numbered

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