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Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments

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Avoiding predation is one of the most important challenges that an animal faces. Several anti-predation behaviours can be employed, yet simply using the presence of conspecifics can be a good signal of safety in an environment with potential predation hazards. Here, we show, for the first time, that past experience of predation causes bumblebees (*Bombus terrestris*) to aggregate with conspecifics, facilitating the identification of safe foraging patches. Bees were trained to differentiate between flowers that harboured predators and flowers that were predator free. When test subjects were subsequently presented solely with the previously predator-infested flower species, there was a significant preference to only land on flowers occupied by other feeding conspecifics. Yet, when safe flowers were made available to subjects previously entrained to discriminate safe from predator-occupied flowers, subjects ignored other bees and the social information potentially provided by them, demonstrating that attraction towards conspecifics is confined to dangerous situations. Our findings demonstrate a previously unknown social interaction in pollinators which may have important implications for plant–pollinator interactions.

1. Introduction

Many animals have the capacity to glean information from other individuals in order to identify and locate potential predator threats. This could either be through direct communication about the threat [1–3], detecting cues left by previous attacks [4–6] or eavesdropping on anti-predator cues [7,8]. Yet by using social information, animals can not only detect where danger lurks, they can also identify where danger is absent. While a dead or distressed conspecific might signify a potential threat, the presence of undisturbed conspecifics could just as importantly indicate an area free of predators revealing a momentarily safe foraging opportunity. Indeed, many animal species aggregate with other individuals in response to predation pressures [9–12], increasing the likelihood of spotting predators [13,14] as well as diluting the risks of being attacked [15–17]. Yet despite the known advantages of group formation, it is still unclear what, if any, behavioural experience facilitates the attraction towards others in response to predation.

Recent research has highlighted the prevalence and importance of predation on pollinators and the consequences for pollination [4,18–24]. Bees face significant predation threats from ambush predators that sit and wait for their prey, often on the flowers themselves. The best studied of these predators are crab spiders (Thomisidae), of which some species have the remarkable ability to change colour to camouflage themselves against the floral background [25,26]. In order to evade these predators, bees can rely on personal information to avoid feeding on risky flowers. For example, because most crab spider predation attempts are unsuccessful [27–29], bees have the opportunity to learn and avoid the location of dangerous floral patches [18]. However, personal sampling of an environment may impose severe fitness costs through predation risks as well as significant reductions in foraging efficiency. Consequently, there may be more benefit in using information from other individuals as a means to bypass these costs.

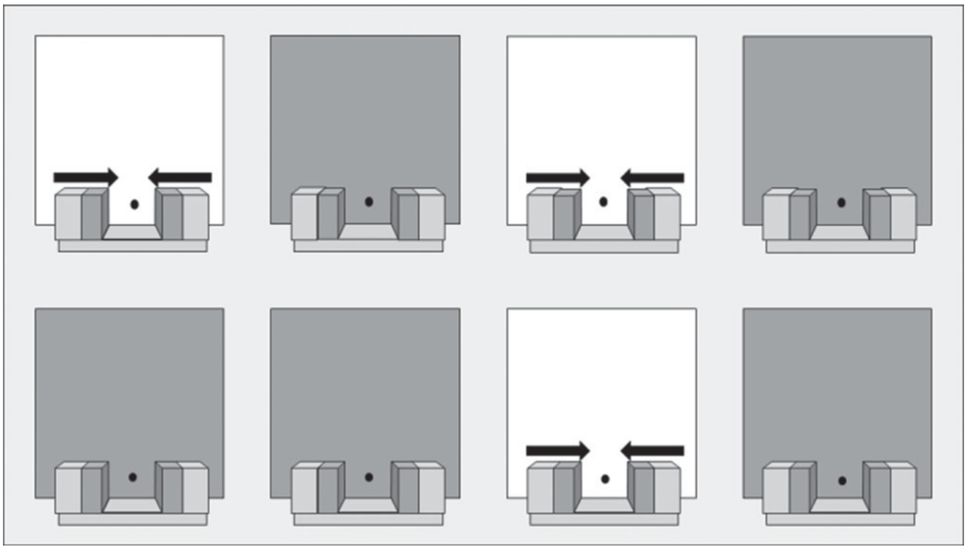

Figure 1. Schematic diagram of the experimental artificial flowers. In this example, landing on white flowers results in the foam pincers closing (as indicated by black arrows), whereas foam pincers remain open when bees land on the alternative colour.

There is evidence that pollinating bees can, indeed, use social information to avoid predation either by identifying sites where other individuals have been attacked [4,30,31] or by relaying the threat to nest-mates [32]. Yet, these social strategies are not fail-safe, because they will only account for instances where a predation attempt has just occurred, therefore leaving bees vulnerable to predators not recently engaged in a predator attack. Here, we propose an alternative scenario, where bumblebees identify safe food sources by joining feeding conspecifics. Following this hypothesis, we predict that through direct experience with a predator, joining behaviour in bees will vary with subsequent predation threats: in dangerous environments, joining is more common than when foraging in safe environments.

2. Methods

(a) Set-up

Three bumblebee (*Bombus terrestris*) colonies (Syngenta, Weert, The Netherlands) were used over the course of the main experiment. Colonies were housed in nest-boxes (29.5 × 40 × 11.5 cm). Each test colony was sequentially attached to a wooden flight arena ($l = 100$ cm, $w = 72$ cm, $h = 73$ cm) by a Perspex tunnel. Within the flight arena, bumblebees could forage from an artificial meadow which consisted of a 2 × 4 vertical array of eight flowers on a grey background (figure 1). Flowers had detachable colour signals which consisted of either yellow or white square plastic panels (7 × 7 cm acrylic, 1 mm thick, coloured white or yellow). Food (sucrose solution 50% w/w) could be accessed through a small circular hole 10 mm above a landing platform (40 × 60 mm). Landing platforms were flanked by two yellow foam-coated pincers (35 × 10 × 20 mm white foam attached to the inside of grey wooden blocks 35 × 10 × 200 mm) which could be rapidly closed to trap a bee briefly without the risk of injury to the bee (figure 1; [33]).

(b) Pre-training

Before training commenced, bees were allowed to familiarize themselves with the floral array within the flight arena. To encourage bees to feed from the flowers, sucrose solution (1 ml) was placed on the landing platforms, which was replenished frequently. In this phase, the detachable yellow and white colour panels were absent, so that flowers appeared the same colour as the grey background. During this pre-training period, test subjects foraged in the arena together with nest-mates.

(c) Training to associate flower colours with reward or predation risk

During the training phase, all bees learned that they would receive a simulated predator attack on flowers of one colour while receiving no such attack on flowers of the alternative colour. Individual bees foraged in the meadow which now consisted of five ‘safe’ yellow flowers and three ‘dangerous’ white flowers. This colour paradigm was reversed for half the bees tested (i.e. white flowers were safe whereas visits to yellow flowers led to subjects being pinched). Every flower contained 5 µl of sucrose solution, this time accessed via the feeding hole. To ensure subjects visited all available flowers, sucrose solution was only replenished after the subject had landed on all the safe flowers. When a test bee landed on a dangerous flower, the foam-covered pincers rapidly closed around the bee and trapped it for 3 s, after which the bee was released, mimicking an unsuccessful predatory attack by a crab spider (Thomisidae) [33].

Aside from flower colour, there were no other cues available to the bee to indicate it was landing on a dangerous flower, paralleling a situation where predators are camouflaged or visually undetectable. When subjects landed on a safe flower, no pinching occurred, and bees were free to feed. After subjects returned to the hive to offload sucrose solution, the positions of the dangerous and safe flowers were changed, so the spatial locations of the flowers could not be learned. Subjects were trained with this paradigm for a minimum of 100 flower landings.

(d) Tests: behaviour in safe versus dangerous environments

Straight after the training period, bees were presented with a predation-free setting, but one set of bees was faced with the flowers of the colour associated with danger during training, whereas another group was presented with the ‘safe’ colour. Bees from the three colonies were randomly allocated to the two treatments. Before releasing the test bee into the arena, we randomly selected one of the eight flowers and allowed three nest-mates (hereafter referred to as ‘demonstrators’) to feed from this flower only. To facilitate the demonstrators to feed from this flower exclusively, we trained them to feed from the selected flower prior to the start of experiments. Moreover, we increased the volume of sucrose solution provided by the flower (from 5 µl to 1 ml of sucrose solution) to ensure demonstrators remained on the flower for the duration of the test. Once all three bees had started feeding on the selected flower, the remaining seven flowers were also made rewarding with the same quantities. When the demonstrators were in place, the test bee, which was being held in the tunnel connecting the arena and nest-box, was released into the flight arena and its first flower choice (i.e. the first flower it landed on) was recorded.

(e) Control: effects of predation risk or reduced rewards?

Visits to 'dangerous' flowers entailed a reduced reward as well as a simulated predator attack. This parallels the natural situation where a spider will typically attack before a bee finishes feeding. However, this means that subsequent changes in behaviour could be attributed to receiving smaller quantities of nectar rewards owing to interruption by predators. To tease apart whether changes in behaviour in subsequent tests occurred as a result of predation or reduced reward, we tested a further control group of 14 bees from a different colony on dangerous flowers in the test phase. In this group, bees were not exposed to simulated predation attempts *during* feeding, but were allowed to complete feeding on the flowers associated with danger before being attacked. All other aspects of training were identical in this 'post-reward predation control group'.

(f) Analyses

To confirm whether subjects in all treatment groups learned to associate the respective flower colours with safety and danger, we compared the proportion of landings on the safe flowers, made in the last 10 choices of the training phase, with chance expectations (0.625), using a two-tailed binomial test.

To establish whether bees would preferentially land on the flower hosting the three demonstrators in the test phase, we then compared the proportion of bees that chose the nest-mate occupied flower against chance expectations (0.125), again calculated using a two-tailed binomial test. To ascertain whether landing choices varied according to the test environment (safe or dangerous), flower colour or training performance (the proportion of correct choices made in the last 10 landings of the training phase), we performed a generalized linear model with a binomial error distribution on data from the two main treatment groups, fitting all factors as predictors. We sequentially dropped non-significant terms until further simplification resulted in a significant decrease in explanatory power of the model, evaluated using chi-squared tests.

If the demonstrators finished feeding before the test subject had made a flower landing, then we excluded that test bee from our analyses. This left us with the following sample sizes: bees tested with the safe flowers: $n = 14$; bees tested with the dangerous flowers: $n = 14$; post-predation reward bees tested with dangerous flowers: $n = 10$. All analyses were carried out using R statistical software (v. 2.12.0).

3. Results

Bees in all treatment groups were highly successful in learning to associate flower colours with safety and danger in the training phase, choosing the safe flowers significantly more than expected by chance, assessed from the last 10 landings in the training phase (mean performance ± s.d.: bees tested on flowers previously associated with safety, 99.3 ± 2.7%, two-tailed binomial test $p < 0.001$; bees tested on flowers previously associated with danger, 98.6 ± 3.6%, $p < 0.001$; post-predation reward control group, 100 ± 0%, $p < 0.001$).

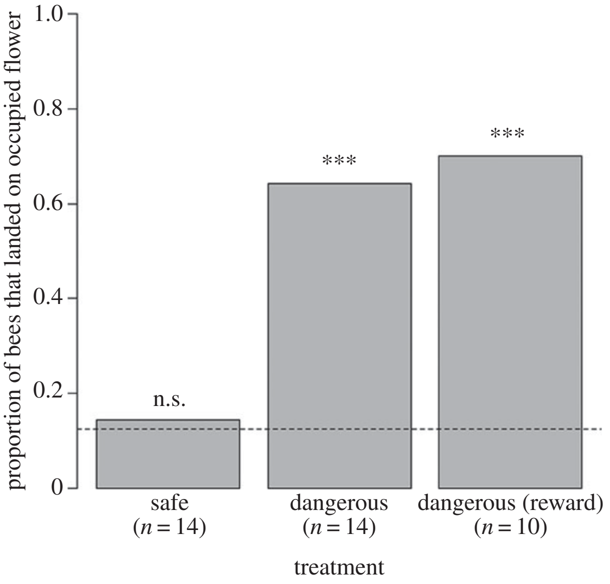

Figure 2. Proportion of bees, in the various treatment groups, that landed on the occupied flower in the test phase. The key comparison is illustrated with the left two columns where bees were presented with the flower colour previously associated with safety and danger, respectively. Bees foraging in a safe environment showed no propensity for joining conspecifics while bees foraging on flowers with a colour previously associated with danger strongly preferred occupied flowers. Subjects in the control group (dangerous (reward)) had been allowed to complete feeding on dangerous flowers during training. Chance expectation of visiting the occupied flower is indicated by the dashed line. n.s. denotes not statistically different from chance; ***$p < 0.001$.

We found that the testing environment (whether bees foraged among flowers linked to safety or danger in the previous phase) had a significant effect on whether bees joined conspecifics or not ($\chi^2 = 7.79$, d.f. = 1, $p < 0.01$). When test subjects were presented with the flower colour associated with danger, there was a significant preference to land on the flower with feeding nest-mates (figure 2; two-tailed binomial test: $p < 0.001$). Most of these subjects displayed hesitation by hovering in front of each unoccupied flower for a few seconds before rejecting it and moving onto the next until they encountered a flower occupied by nest-mates where they landed and fed. However, when bees were presented with the 'safe flowers', subjects generally showed no hesitation and landed on the first flower they came across, regardless of whether it was occupied by other bees or not. In this treatment group, only two of the 14 bees landed on the flower occupied by conspecifics, which is entirely in line with chance expectation (figure 2; two-tailed binomial test: $p = 0.692$) demonstrating that bees in this situation ignored social information and chose to land on flowers at random spatial positions when they had learnt that this particular flower colour was not associated with danger. Flower colour ($\chi^2 = 1.88$, d.f. = 1, $p = 0.17$) and training performance ($\chi^2 = 0.4$, d.f. = 1, $p = 0.53$) had no significant effect on the landing choices of bees.

When bees received equal amounts of sucrose solution on dangerous and safe flowers in the training phase, subjects still significantly preferred to join the flower occupied by other conspecifics when confronted with 'dangerous flowers' (figure 2; two-tailed binomial test: $p < 0.001$), suggesting that joining behaviour occurs solely in response to danger and is not a result of receiving less sucrose solution on flowers associated with danger.

4. Discussion

Our findings clearly demonstrate that bumblebees choose to feed with other conspecifics when previous experience indicated that they were facing a perilous foraging situation. It is clear that this social information use occurs in response to danger alone, and is not a result of receiving less food because of an attack, because bees still chose to join conspecifics after they had been trained to learn that dangerous and safe flowers were equally rewarding. When no threat is detected, social information is ignored, demonstrating that bumblebees actively decide when to use social information according to the environmental context.

Many cases of social information use are underpinned by simple associations, whereby conspecifics become a predictor of a rewarding stimulus [34–37]. From a mechanistic perspective, the social foraging experience that all bees experienced in the pre-training phase may have led to the formation of positive associations with conspecifics, potentially explaining why bumblebees were attracted to nest-mates under conditions of predation threat. However, subjects that were presented with the safe flowers had also previously foraged with conspecifics, yet showed no such attraction towards nest-mates, suggesting that these associations manifest only under conditions where it is adaptive.

In nature, many flower species (particularly in the Asteraceae family) contain multiple nectaries, where the available nectar rewards are not immediately depleted by a single visitor and several pollinators can feed simultaneously (figure 3). This foraging scenario parallels the pre-training phase (which all treatment groups experienced), where individuals had the opportunity to feed together with conspecifics in absence of competition. However, individual flowers of many species can be depleted by a single visit, and in such a scenario, perhaps previous competition with conspecifics could result in bees responding differently to social information in risky environments.

The behavioural strategy we observe here is consistent with existing social learning theory which predicts that social information should only be used in specific fitness enhancing circumstances [38–40]. When information is not costly to acquire (such as landing at a flower where there is no predation risk), it is more beneficial to use personal information than to follow conspecifics. This is because, typically, more food resources are acquired by feeding alone than sharing the resource with multiple individuals. Conversely, when information acquisition imposes a high risk, such as feeding on a flower potentially harbouring predators, it is more beneficial to use social rather than to use personal information, even if this carries a significant cost in food intake. For example, previous research demonstrates that bumblebees that encounter flowers with which they are already familiar, avoid flowers occupied by conspecifics, yet conversely seek out conspecifics when foraging from unfamiliar flower types, most likely in response to the costs involved with personal exploration, such as trial-and-error sampling [41,42]. However, we should be cautious in placing our findings in a similar theoretical framework, because competition between conspecifics for food was not a feature of this experiment.

Figure 3. Multiple pollinators, of the same and different species, are often observed feeding together on inflorescences with many nectaries potentially leading to bees acquiring the social pre-foraging experience which facilitates joining behaviour in dangerous environments. (*a*) *Bombus terrestris* (or *lucorum*) foragers feed from an ornamental thistle (*Cirsium rivulare*) (photo credit: Richard Burkmar, with permission). (*b*) *B. terrestris* (or *lucorum*) and *B. pascuorum* individuals collect resources from a creeping thistle flower (*Cirsium arvense*) (photo credit: Stephan Wolf, with permission). (*c*) *B. terrestris* (or *lucorum*) feed together on a globe thistle (*Echinops ritro*; photo credit: Kiran Ravilious, with permission). (Online version in colour.)

Previously, it has been shown that the non-consumptive effects of predators (e.g. through avoiding flowers on which a predator attempt was made and subsequently all flowers of a similar appearance [18]) can have significant influences on plant fitness and the dynamics of pollinator–plant interactions [20,24,43]. However, our results suggest that such generalized avoidance behaviour might be counteracted to some extent by using social information, because bees readily resumed foraging activity on flowers they previously perceived to be dangerous after joining conspecifics. Thus, social information use may have profound and complex implications for pollination services.

In closing, our study adds to the body of evidence demonstrating the importance of social information in antipredator behaviour by revealing a hitherto unknown social predator avoidance tactic in pollinators. Furthermore, our findings strengthen the observation that the use of social information is dictated by conditions in which they are most useful [44] rather than following a hard-wired set of behavioural rules.

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Data accessibility. Data supporting this paper are available as electronic supplementary material.

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