



Can bees simultaneously engage in adaptive foraging behaviour and attend to cryptic predators?



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Bees foraging for nectar often have to discriminate between flowers with similar appearance but different nectar rewards. At the same time, they must be vigilant for ambush predators, such as crab spiders, which can camouflage themselves on flowers. We investigated whether bees, *Bombus terrestris*, can efficiently discriminate similar flower colours while exposed to predation threat from cryptic predators. Bees were individually tested in tightly controlled laboratory experiments using artificial flowers whose nectar supply was administered with precision pumps. Predation risk was simulated by automated crab spider 'robots' that captured bees for a limited duration without injuring them. Bees' behaviour was monitored by a 3D video tracking system. We experimented with both cryptic and conspicuous spiders, finding that bees had no difficulty avoiding conspicuous spiders while still foraging adaptively. Conversely, they prioritized predator avoidance at the expense of maximizing energy intake when faced with detecting cryptic predators and a difficult colour discrimination task. This difference in behaviour was not due to cognitive limitations: bees were able to discriminate between similar flower types under predation risk from cryptic spiders when choosing the safe flower type incurred a gustatory punishment in the form of bitter quinine solution. However, this resulted in bees incurring substantially higher costs in terms of floral inspection times. We conclude that bees have the capacity to attend to difficult foraging tasks while simultaneously avoiding cryptic predators, but only do so when avoidance of gustatory punishment justifies the increased costs.

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Animals are exposed to a constant flow of complex sensory input. Foragers, for example, must prioritize information relevant to important tasks, such as locating the most rewarding food items or detecting predators (Milinski 1984; Godin & Smith 1988; Clark & Dukas 2003). For many animals, such as bees, foraging and visual search often require a trade-off between attending to the foraging target (e.g. flowers) and focusing on potential danger in the environment (e.g. sit-and-wait predators on flowers). A foraging bee will spend most of its time choosing between visual targets (flowers) that vary in colour, shape and pattern, and is under constant pressure to select the most rewarding flowers while minimizing predation risk and energetic costs (Chittka & Menzel 1992). The task can be challenging and highly dynamic since there are distractor flowers, that is, other plant species with different traits (Schaefer & Ruxton 2009) and camouflaged predators in the field

(Morse 2007). Many plant species, such as those in the orchid family, have flowers that resemble the appearance or odour of co-occurring, rewarding species to attract pollinators (Dafni 1984; Roy & Widmer 1999). Moreover, predators can use the attractiveness of flowers to lure their prey. For example, crab spiders (Araneae: Thomisidae) are sit-and-wait predators that ambush pollinators, such as bees, on flowers (Chittka 2001; Insausti & Casas 2008). Some species of crab spiders can reversibly change their body colour to match that of the flower on which they are hunting (Morse 1986). They even preferentially hunt on high-quality flowers (Morse 1986), which are also preferred by foraging bees (Menzel et al. 1993; Heiling et al. 2004).

We have a good understanding of the individual problems facing foraging bees: how they choose between different flowers (Giurfa & Lehrer 2001; Shafir et al. 2003; Chittka & Raine 2006) and how they interact with predators (Heiling & Herberstein 2004; Dukas 2005; Reader et al. 2006). Bees can associate food rewards with specific floral traits, such as colour, and can successfully discriminate between even subtle differences in traits to maximize foraging efficiency (Dyer & Chittka 2004a). Furthermore, bees are able to learn to avoid both individual flowers harbouring predators and sets of flowers of a given type (colour)

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associated with predation risk (Ings & Chittka 2008, 2009; Jones & Dornhaus 2011). However, it is not known how bees perform when exposed to both flower colour discrimination and predator avoidance tasks simultaneously, a situation that bees must naturally face. Evidence from field studies suggests that bees may choose to avoid a patch harbouring predatory crab spiders (Dukas & Morse 2003), and laboratory studies indicate that bees may also choose to switch to a less risky flower species (Ings & Chittka 2009; Jones & Dornhaus 2011). Therefore, we asked whether bees have the perceptual and cognitive processing power to carry out such tasks simultaneously.

Early work on insects seemed to indicate that pollinators can efficiently deal with only one task at a time (Lewis 1986), and indeed animals with substantially larger brains have extensive capacity limitations in perceptual processing resulting in significant costs associated with performing the precise discrimination of more than one stimulus dimension (Kahneman 1973; Pashler 1998; Dukas 2009). For example, in humans there are severe information-processing consequences when one must divide attention between two forms of visual input as simple as shape and orientation, such that only one task can be attended to at a time (Joseph et al. 1997). Therefore, we might expect such capacity limitations to be all the more important in much smaller animals with concomitant smaller nervous systems, such as bumblebees.

In this study we asked whether bumblebees are able to maximize energy gains by solving a difficult colour discrimination task while simultaneously exposed to predation threat from camouflaged or conspicuous predators. First, we exposed bees to an ecologically relevant scenario in which they foraged in an artificial meadow with two visually similar flower types differing in reward quality. Visiting the highly rewarding flower type was risky because 25% of flowers harboured predatory crab spider models. If bees are able to solve colour discrimination and predator avoidance tasks simultaneously we predicted that they would visit the highly rewarding species but avoid individual flowers that are risky. Our null hypothesis is that bees are unable to attend to two difficult tasks simultaneously and that (1) bees would prioritize predator detection and avoidance when predators are camouflaged and (2) they would continue to maximize energy gains when predators are highly conspicuous. Second, because bees did not simultaneously focus on predator avoidance and maximizing energy gains we asked whether this is a result of limited cognitive capacity. In this experiment we manipulated the balance of risk and reward beyond that naturally encountered by incorporating gustatory punishment into the colour discrimination task. Under this scenario we predicted that bees would be unable to focus on predator avoidance as well as discriminating between rewarding and distasteful flowers. Ultimately, we hypothesized that such limitations in sensory processing would increase indirect trait-mediated effects of predators on plants when predators are cryptic, that is, bees would alter their foraging preferences when exposed to predation threat from camouflaged predators.

METHODS

Study Animals

Three colonies of bumblebees, *Bombus terrestris*, from a commercial supplier (Syngenta Bioline Bees, Weert, Netherlands) were used in the experiment. All the bees were individually tagged with number tags (Christian Graze KG, Weinstadt-Endersbach, Germany). Colonies were kept at room temperature (ca. 23 °C) and on a 12:12 h light:dark cycle (light on at 0800 hours). Sucrose solution (50%, v/v) and pollen were provided ad libitum. A total of 54 foragers were used in the experiments.

Experimental Apparatus

All experiments were conducted in a wooden flight arena (1.0 × 0.72 m and 0.73 m high) with a UV-transmitting Plexiglas lid. Two twin lamps (TMS 24 F with HF-B 236 TLD [4.3 kHz] ballasts, Philips, The Netherlands) fitted with Activa daylight fluorescent tubes (Osram, Germany) were suspended above the flight arena to provide controlled illumination. Artificial flowers (7 × 7 cm acrylic, 1 mm thick) were arranged in a four by four vertical grid on one end wall of the arena on a grey background (Appendix Fig. A1). The opposite wall contained an entrance hole through which the bees could enter the arena from the colony. Bees were able to get access to rewards (sucrose solution) through a hole which was 10 mm above a wooden landing platform (40 × 60 mm). A constant flow (mean ± SEM = 1.85 ± 0.3 µl/min) of sugar solution (reward) was supplied to each flower from individual syringes attached to two multisyringe infusion pumps (KD Scientific, KD220, Holliston, U.S.A.). At each flower, the solution was delivered via silicone tubing ending in a 26G syringe needle (BD Microlance Drogheda, Ireland; 0.45 × 13 mm) temporarily held in place in front of the hole in the wall by reusable adhesive (Blue Tack, Bostick, U.S.A.). A maximum droplet volume of 4.70 ± 0.3 µl could be reached before it fell into a 'waste pot' which was not accessible to bees (thus mimicking a flower that had been emptied by a bee). This avoided unvisited flowers from becoming excessively rewarding and the slow refill rate prevented bees from revisiting a flower immediately after removing the reward. Revisits did occur (mean ± SEM = 3.59 ± 0.4 per flower) as we had a limited number of flowers in the arena, but these typically occurred after the bees had visited several other flowers in the arena first (mean ± SEM = 130.84 ± 14.7 s between revisits). Robotic 'spider arms' (custom-built by Liversidge & Atkinson, Romford, U.K.) covered with sponges were set up at the base of the flowers to simulate predation attempts. The trapping mechanism enabled us to capture bees without causing physical damage. 'Dangerous flowers' were fitted with life-sized crab spider, *Misumena vatia*, models (length = 12 mm, made from Gedeo Crystal resin) placed on the flowers above the feeding hole. The flight behaviour and position of bees were recorded during the experiment with three-dimensional coordinates of bee positions being calculated 50 times/s using two video cameras connected to a computer running Trackit 3D software (BIOBSERVE GmbH, Bonn, Germany).

Pretraining

All bees were allowed to fly in the flight arena without any presentation of floral signals for at least 1 day before the experiment. A constant flow (mean ± SEM = 1.85 ± 0.3 µl/min) of 50% (v/v) sucrose solution was given as a food reward. Only bees that left the colony and fed on the flowers consistently for at least three consecutive foraging bouts were used in the experiments.

Experimental Design

Experiment 1: discriminating reward quality under predation risk

In this experiment we asked whether bees exposed to an ecologically relevant scenario were able simultaneously to solve a colour discrimination task to maximize energy gains while avoiding conspicuous or camouflaged predators. Bees could choose between two types of flowers that were similar shades of yellow to human observers (neither shade of yellow reflected appreciable amounts of UV light and therefore both colours were green to bees, i.e. they stimulated predominantly the bees' green receptors; Fig. 1a). The flower colours were chosen so that bees could distinguish between them, but only with significant difficulty (see

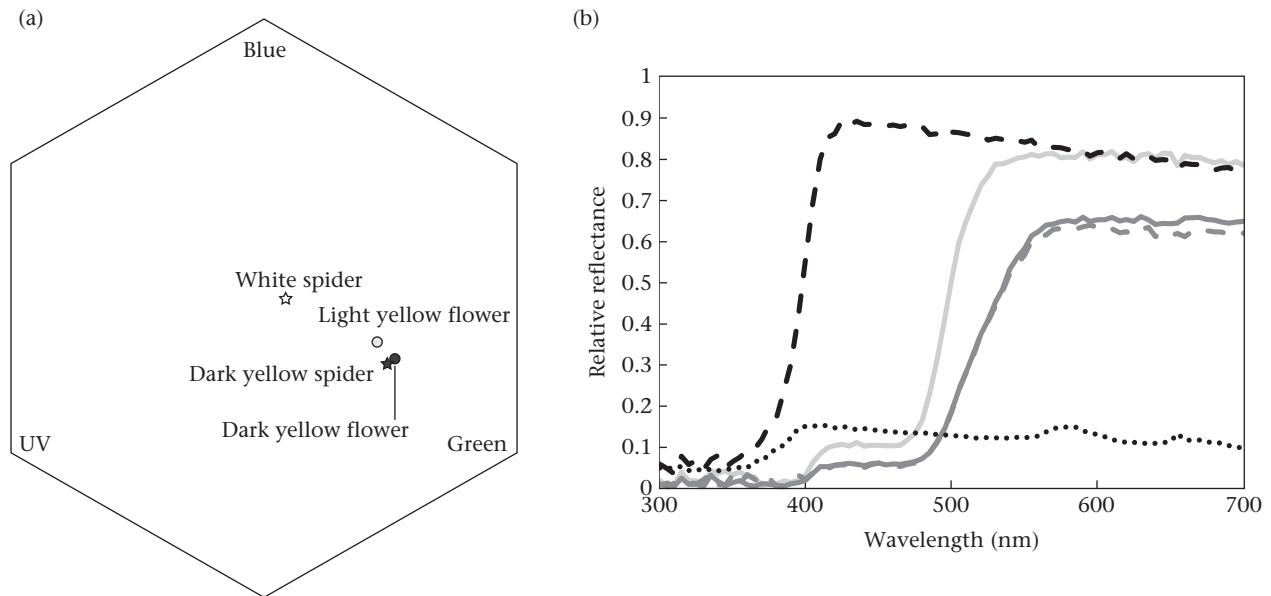


Figure 1. (a) Appearance of yellow flowers (circles: light grey for light yellow and dark grey for dark yellow) and spiders (stars: white for conspicuous spiders and dark grey for cryptic spiders) in bee colour space (calculated using *Bombus terrestris* colour receptor sensitivity functions in Skorupski et al. 2007) relative to the grey background colour (centre of the hexagon). Positions of the colour loci in the hexagon indicate excitation differences of the three bee colour receptors. The corners of the hexagon labelled UV, Blue and Green correspond to hypothetical maximum excitation of one receptor combined with zero excitation in the two others. The angular position in the hexagon (as measured from the centre) is indicative of bee subjective hue. Loci that are close together appear similar to bees and loci that are far apart appear different. (b) Spectral reflectance curves of artificial flowers, spiders and the grey background of the meadow. The dashed lines represent spiders (dark grey = dark yellow spiders and light grey = white spiders), solid lines flowers (dark grey = dark yellow flowers and light grey = light yellow flowers) and the dotted line represents the grey meadow background.

Appendix. The darker shade of yellow (which was associated with high-quality rewards) was distinguished from the lighter yellow shade (low-quality rewards or penalties) by a colour hexagon difference of only 0.084 units, which indicates poor discriminability according to previous work (Dyer & Chittka 2004a). We also tested experimentally that the two colours were distinguishable, but with difficulty, for bees (Appendix).

The high-quality (dark yellow) flowers carried a risk of predation from either conspicuous or cryptic 'robotic spiders' (Ings & Chittka 2008). Twenty-five per cent of the flowers harboured a spider. Conspicuous spiders were of white appearance to human observers. They absorbed UV to some extent (Fig. 1b), and they therefore appeared blue-green to bees. However, some of the white spiders' reflectance still extended into the highly sensitive UV-receptor's domain below 400 nm. These spiders' colour loci therefore appeared very close to the uncoloured point ('bee-white', in the centre of the colour hexagon; Fig. 1a). They were distinguished by a colour contrast (colour hexagon distance) of 0.439 units from the dark yellow flower substrate, indicating a high level of conspicuousness. The contrast provided specifically to the bumblebees' green receptor is also important, since this receptor feeds into the motion-sensitive system and is thus often crucial in target detection (Dyer et al. 2008). Green receptor contrast between white spiders and their dark yellow flower backdrop is likewise large (0.104 on a scale of 0 to 1 where zero equals no contrast) indicating high detectability of the white spiders in terms of both colour contrast and green contrast. Conversely, cryptic spiders were dark yellow like the flowers on which they were placed, and both colour contrast (0.036 hexagon units) and green contrast (0.004) values were very low, indicating poor detectability of these spiders. As in a previous study (Ings & Chittka 2008) the spiders were only detectable using shape-from-shading cues.

Individual bees ($N = 34$ randomly selected from two colonies) were initially trained to distinguish between the shades of yellow, with the darker yellow flowers containing high-quality

rewards (50% v/v sucrose) and the lighter yellow flowers providing low-quality rewards (20% v/v sucrose). Training continued until bees made a minimum of 200 flower choices. To reach this criterion, bees returned to the nest to empty their crops three to five times (mean \pm SEM number of foraging bouts: cryptic = 4.9 ± 0.7 ; conspicuous = 3.7 ± 0.3 ; total duration: cryptic = 45.27 ± 3.71 min; conspicuous = 40.93 ± 3.43 min). All bees were allowed to complete their final foraging bout and return to the nest under their own volition to avoid unnecessary handling that may have influenced their predator avoidance behaviour. To prevent bees from learning the locations of high-reward flowers the positions of all flowers were randomly reassigned between every foraging bout. Redistribution of flowers and their food supply (syringe needles at the end of the silicone tubing) took under 5 min, and in most cases was achieved before bees had emptied their honey crops in the nest and returned to the nest entrance tube. After initial colour discrimination training, bees were randomly assigned to one of two groups exposed to predation risk on high-quality flowers (25% of flowers harboured robotic spiders) by either conspicuous (white spider model on dark yellow flower; Fig. 1) or cryptic (dark yellow spider model on dark yellow flower) spiders ($N = 17$ in each group). Predator avoidance training lasted for a further 200 flower choices (mean \pm SEM total duration of avoidance training: cryptic = 32.52 ± 2.91 min; conspicuous = 41.32 ± 5.09 min). Every time a bee landed on a high-reward flower with a spider (dangerous flower) it received a simulated predation attempt whereby the bee was held by the arms of a robotic crab spider for 2 s. This emulates natural spider attacks on bumblebees where bees are grasped by the raptorial forelegs of the spider but manage to escape, avoiding immobilization by the spider's bite. As in colour discrimination training, locations of all flowers were randomly reassigned between foraging bouts (mean \pm SEM number of foraging bouts: cryptic = 4.9 ± 0.8 ; conspicuous = 4.2 ± 0.3).

Experiment 2: discriminating gustatory punishment and reward under predation risk

To determine whether the apparent inability of bees to solve colour discrimination and cryptic predator avoidance tasks simultaneously was due to limitations in sensory processing or attention, we conducted a second experiment in which the balance of risk and reward was adjusted beyond that naturally encountered. In this experiment, a third group of bees ($N = 10$ from colony 3) was given an additional incentive to discriminate between the shades of yellow flower by replacing the low-quality rewards with a form of gustatory punishment, a distasteful (bitter) quinine hemisulphate solution that bees rapidly learn to avoid (Chittka et al. 2003). This solution contained no sucrose. Bees do not ingest this solution and abort flower visits immediately upon tasting it. It has been demonstrated empirically that such punishment generates much stronger discrimination than simply rewardless flowers that need to be distinguished from rewarding flowers (Chittka et al. 2003). Thus, bees were initially trained to distinguish between dark yellow rewarding flowers containing 50% v/v sucrose solution and light yellow distasteful flowers containing 0.12% quinine solution. After colour discrimination training for 200 flower choices (see experiment 1, mean \pm SEM total duration = 37.79 ± 3.78 min) bees were then exposed to predation risk (25%) from cryptic spiders (the hardest predator avoidance task) on the rewarding (dark yellow) flowers for a further 200 flower visits (mean \pm SEM total duration = 31.75 ± 2.33 min). Locations of flowers were randomly reassigned between every foraging bout (mean \pm SEM number of bouts: colour discrimination training = 3.7 ± 0.3 ; predator avoidance training = 4.4 ± 0.4).

Data Analysis

Individual bees' preferences for highly rewarding flowers (dark yellow) were calculated from their final 30 flower choices of the colour discrimination training phase in both experiments. These preferences were then used to determine predator avoidance

during the training phase, where bees were exposed to predation risk (pairwise comparisons using paired t tests or Wilcoxon signed-ranks tests if data violated the assumptions of the t test; all tests were two tailed). For example, under the null hypothesis of no spider avoidance, a bee that chose highly rewarding flowers at a frequency of 80% at the end of training would be expected to choose dangerous flowers (two dangerous flowers out of eight highly rewarding flowers) with a probability of $0.8 \times 0.25 = 0.2$.

The time bees spent investigating and feeding on flowers was calculated from time and position data recorded using Trackit 3D software. Investigating zones were 7 cm long, 9 cm wide and 9 cm high around landing platforms, and the feeding zones were 4.5 cm by 1 cm by 1 cm from the feeding hole. Investigating zones were set based on the visual angles of bumblebees where bees were able to detect both flower signals and predators using colour contrast (Spaethe et al. 2001) and feeding zones were based on observation of the position bees take while feeding at the flowers. Only instances when bees landed and fed on the flowers were considered as choices. Investigation duration was quantified as the time spent in the investigation zone before landing on a flower or choosing to depart (when bees rejected the flowers without landing). Data were analysed using R v. 2.15.1 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and JMP v. 7 (SAS Institute Inc., Cary, NC, U.S.A.). Four bees that lost motivation (i.e. stopped foraging) during training were excluded from the analysis (two per group in experiment 1).

RESULTS

Discrimination Learning

All bees commenced training without a preference (Fig. 2) for either shade of yellow, irrespective of reward level or punishment (mean \pm SEM percentage of dark yellow flowers selected during the first 30 choices: conspicuous spider group = 50.0 ± 2.25 ; cryptic spider group = 48.7 ± 5.4 ; quinine group = 49.3 ± 3.9 ;

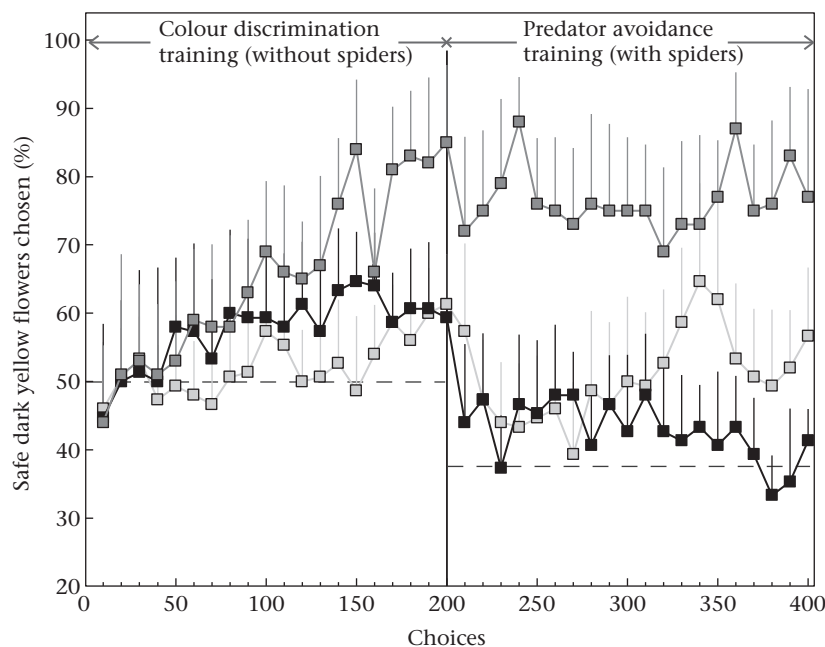


Figure 2. The mean (plus upper 95% confidence interval) percentage of safe high-reward flowers (without spiders) chosen during consecutive blocks of 10 trials during colour discrimination and predator avoidance training in experiments 1 and 2. Black represents bees exposed to cryptic spiders and light grey bees exposed to conspicuous spiders in experiment 1, while dark grey represents bees in experiment 2 that were exposed to cryptic spiders and quinine punishment in distractor flowers. The dashed lines represent the expected percentage of high-reward flowers chosen if bees foraged completely at random, i.e. with no preference for either flower type.

ANOVA: $F_{2,37} = 0.029$, $P = 0.971$; one-sample t test against random visits [50%] on pooled data for all groups of bees: $t_{39} = -0.285$, $P = 0.777$; Fig. 2). However, by the end of the colour discrimination training, bees in experiment 1 had developed a slight, but significant preference (Fig. 2) for the dark yellow flowers (mean \pm SEM = $59.7 \pm 2.0\%$ [pooled data for both groups] dark yellow flowers selected during the last 30 choices; one-sample t test [against 50%]: $t_{29} = 4.853$, $P < 0.001$). Furthermore, colour discrimination was significantly greater in experiment 2 in which bees encountered bitter quinine in the light yellow flowers (mean \pm SEM = $83.3 \pm 4.0\%$ dark yellow flowers selected: t test [experiment 1 versus experiment 2]: $t_{38} = -5.710$, $P < 0.001$; Fig. 2).

Discriminating Reward Quality under Predation Risk

Both groups of bees in experiment 1 rapidly learnt to avoid robotic spiders (Fig. 3), although the initial avoidance response was stronger when spiders were conspicuous (Fig. 3; Mann–Whitney U test: $U = 197.5$, $N_1 = N_2 = 15$, $P < 0.001$). By the end of training, both groups visited virtually no dangerous flowers (median percentage during the last 30 choices for both groups = 0.0 and the interquartile range = 3.3; Wilcoxon signed-ranks test: $T = 4.790$, $N = 30$, $P < 0.001$; Fig. 3). However, the two groups differed significantly in their ability to discriminate between similar shades of yellow flowers simultaneously to maximize their energy intake (mean \pm SEM percentage of safe, highly rewarding flowers chosen during the last 30 choices: cryptic spiders = 36.7 ± 2.8 ; conspicuous spiders = 52.7 ± 4.4 ; t test: $t_{28} = 3.097$, $P = 0.004$; Fig. 2). Bees encountering conspicuous spiders regained their slight preference for high-reward flowers (one-sample t test against random visits [37.5%]: $t_{14} = 3.483$, $P = 0.004$) whereas bees exposed to cryptic spiders failed to discriminate between high- and low-reward flower types and foraged from all safe flowers at random (one-sample t test against random visits [37.5%]: $t_{14} = -0.300$, $P = 0.769$).

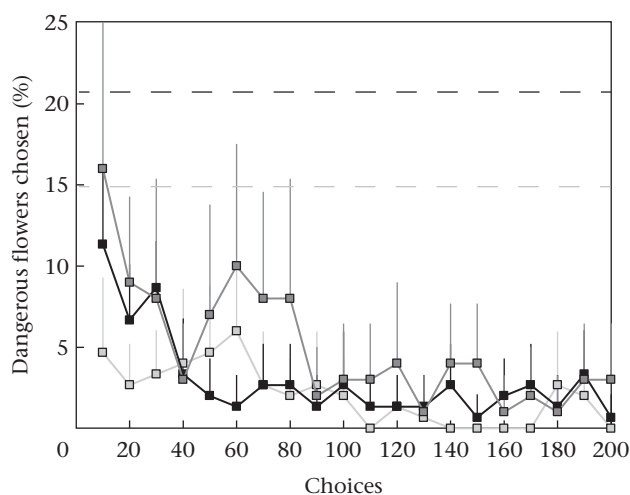


Figure 3. The mean (plus upper 95% confidence interval) percentage of dangerous flowers chosen during consecutive blocks of 10 trials during avoidance training in experiments 1 and 2. Black represents bees exposed to cryptic spiders and light grey bees exposed to conspicuous spiders in experiment 1, while dark grey represents bees in experiment 2 that were exposed to cryptic spiders and quinine punishment in distractor flowers. The dashed lines represent the avoidance thresholds (percentage of dangerous flowers expected to be chosen if bees ignored spiders and visited all dark yellow flowers at their learnt preference level) for experiments 1 (light grey) and 2 (dark grey). Values that lie below these lines indicate significant avoidance of dangerous flowers.

Exposure to predation risk had no significant impact on the average time spent inspecting flowers (comparison of mean duration before and after spiders were added; paired t test: conspicuous spider group: $t_{14} = 0.003$, $P = 0.998$; cryptic spider group: $t_{14} = 1.354$, $P = 0.197$; Fig. 4).

Discriminating Gustatory Punishment and Reward under Predation Risk

When failure to choose the correct shade of yellow flower incurred a gustatory punishment (distasteful quinine), rather than a lower quality reward, bees were able simultaneously to solve the colour discrimination task and avoid cryptic predators on the rewarding flower type (Figs 2, 3). Although bees initially visited dangerous flowers at random (first 10 choices in Fig. 3), they rapidly learnt to avoid cryptic spiders after experiencing simulated predation attempts (median percentage during the last 30 choices = 3.3 and the interquartile range = 3.3; Wilcoxon signed-ranks test: $T = 2.805$, $N = 10$, $P = 0.005$; Fig. 3). Furthermore, they were able simultaneously to maintain their high level of colour discrimination (mean \pm SEM percentage of safe, highly rewarding flowers chosen during the last 30 choices = 78.7 ± 5.0 ; one-sample t test against random [37.5%]: $t_9 = 8.276$, $P < 0.001$; Fig. 2).

Once exposed to predation threat, bees spent 28% more time inspecting flowers before making their choices than they did before learning about predation risk (paired t test: $t_9 = 7.442$, $P < 0.001$; Fig. 4). This increase in investigation time was also significantly greater than observed for bees exposed to conspicuous spiders in the first experiment ($t_{23} = 3.697$, $P = 0.001$; Fig. 4).

DISCUSSION

In this study we presented bees with two natural tasks that potentially lead to attentional competition (Kahneman 1973; Pashler 1998; Dukas 2009). The first task was to maximize energy intake by using subtle differences in flower colour to differentiate between reward qualities. The second was to detect and avoid predators that were either conspicuous or cryptic. We found that when predator detection was difficult, bees prioritized predator avoidance over floral colour discrimination. However, when bees were forced to make the colour discrimination by use of a gustatory punishment in the distractor flowers, bees were able to solve both colour discrimination and predator avoidance tasks simultaneously. Solving both tasks did not come for free, since bees incurred substantially increased inspection times when trying to avoid both predators and quinine penalties. Therefore, we argue that prioritization of predator detection when predators are cryptic is a strategy employed by bees, rather than being due to a fundamental limitation to attend to only one task at a time (Lewis 1986). As in other tasks, for example sensorimotor learning (Chittka & Thomson 1997) or the formation of visual object concepts (Avargues-Weber et al. 2012b), it appears that bees can in principle juggle more than a single task, but typically do so at increased temporal costs (Chittka & Thomson 1997). Our results therefore show that bees employ a degree of attentional modulation depending upon the fine balance between risks and rewards (Spaethe et al. 2006; Giurfa 2013).

It has recently been suggested that bumblebees might carry out restricted parallel visual search, that is, where the whole visual field is processed simultaneously and the targets ‘pop out’ from distractors (Morawetz & Spaethe 2012). This being so, bees in our study might have focused attention on flowers that matched their search image (i.e. dark yellow flowers = highest reward in training). Conspicuous predators are highly salient and bees strongly avoided dangerous flowers right from the beginning of

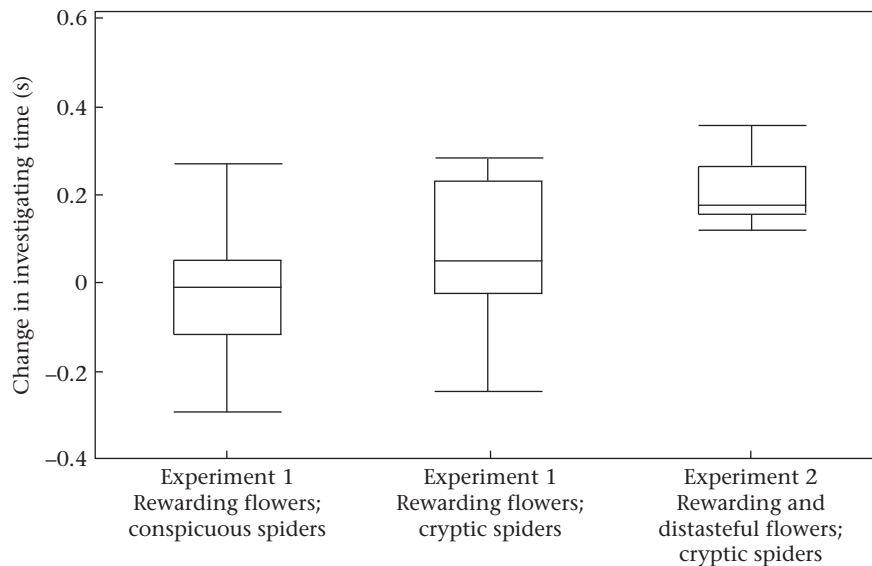


Figure 4. Difference in floral investigation time between colour discrimination training and predator avoidance training (average investigating time per flower after adding spiders minus average time before adding spiders). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range.

training (Fig. 3). It is therefore likely that safe (plain) dark yellow flowers were processed as targets and light yellow flowers and dangerous flowers were processed as distractors. In this case bees would only need to compare each flower against one search image and therefore attend to only a single visual search task.

A different pattern emerged when spiders were cryptic. Owing to lack of contrast between spiders and background flowers (Fig. 1) we would expect bees initially to view dangerous flowers as desirable target flowers. Indeed, this is exactly what was observed during the first few choices made by bees in the cryptic spider group that chose significantly more dangerous flowers than bees in the conspicuous spider group during their first 30 choices (Fig. 3). Despite this, bees exposed to cryptic spiders did learn to avoid dangerous flowers, indicating that they had developed a new search image for cryptic spiders (Ings et al. 2012). Therefore, we are led to ask how bees process each flower during visual search. Avoiding dangerous flowers and maximizing energy gains would require a two-step process owing to the similarity between target and distractor flowers: bees could assess flowers as either spider-infested or spider-free and then discriminate between flower colours, or vice versa. This sequential decision making could make the assessment more costly in terms of time than the one-step process necessary for avoiding conspicuous spiders (Spaethe et al. 2006; Ings & Chittka 2008). Our results showed that bees encountering cryptic spiders prioritized predator avoidance at the expense of discriminating floral reward quality of the remaining safe flowers. To understand whether this failure to attend to both tasks is due to principal limitations in sensory processing and cognitive abilities (Lewis 1986; Dukas 2009) we need to consider how bees responded to predation threat in experiment 2 when they were strongly incentivized to discriminate between the similar shades of yellow.

When one flower colour was associated with a positive value (sucrose reward) and the other with a negative value (quinine), bees were able to maintain two value-defined categories for the task (light yellow = punishment, dark yellow = reward). As a result, discrimination between light and dark yellow flowers was substantially better than in experiment 1 (Fig. 2). Furthermore, bees also maintained this high level of discrimination under predation threat from cryptic spiders on the rewarding flowers. This difference in response compared to bees in the cryptic spider group in

experiment 1 shows that bees are able simultaneously to solve both complex visual search tasks given sufficient incentive. However, this incurs elevated temporal costs, which indicates a sequential assessment of the flowers for safety (spider presence/absence) and reward level (by colour), as predicted by assuming that bumblebees are using restricted parallel visual search (Spaethe et al. 2006; Morawetz & Spaethe 2012). Therefore, we are led to conclude that bees are able to divide their attention between two complex visual search tasks in two different contexts. This result is all the more remarkable given the failures of divided attention in related tasks in birds (Dukas & Kamil 2000) and humans (Joseph et al. 1997).

An alternative explanation to divided attention is that bees categorized (Srinivasan 2010; Avargues-Weber et al. 2012a) flowers into 'good' or 'bad' types, irrespective of whether penalties were predation attempts or of a gustatory nature. Light yellow flowers, which contained quinine in experiment 2, could be classed as poor foraging options, as could dark yellow flowers harbouring cryptic spiders. Dark yellow flowers without spiders could be classed as desirable foraging options. Thus, one might assume that a bee only needs to follow a simple rule: if the flower matches the search image for 'good' then visit, otherwise avoid. However, the increased inspection times in the face of two undesirable types of flowers indicate that bees actively discriminate against both types of 'bad' flowers, that is, a scenario based on visual target categorization would still require the memorization of three search images being employed simultaneously.

Finally, our results have interesting implications for the temporal costs of decision making under natural conditions. Why did bees under predation threat choose not to engage in efficient foraging when solving the colour discrimination task would have meant feeding from flowers bearing more than twice the energetic rewards? In experiment 2 bees had to spend a significantly (ca. 28%) longer time inspecting flowers under predation threat from cryptic spiders (Fig. 4). Inspection of flowers is carried out in flight, which is an energetically demanding activity (Kacelnik et al. 1986; Hedenström et al. 2001), so even small increases in inspection times are likely to bear high energetic costs to bees. The increased inspection times observed in experiment 2 can largely be attributed to the detection and avoidance of cryptic spiders (Ings & Chittka

2008; Ings et al. 2012) which can lead bees to shift to alternative safe flower types if they are as rewarding as risky flowers (Ings & Chittka 2009). Furthermore, theoretical models (Jones 2010) predict that bees can maximize lifetime foraging gains by switching to lower quality flowers when highly rewarding flowers have a higher level of predation risk. Indeed, bumblebees do appear to make optimal choices under laboratory conditions when predation risk is simulated (Jones & Dornhaus 2011), although field studies on honeybees, *Apis mellifera*, show that they are less inclined to avoid risky but highly rewarding patches (Llandres et al. 2012). While these differences could represent species-specific responses, they are equally likely to be caused by differences in the balance of risk and reward as well as the difficulty of the visual search tasks involved. In the study by Jones & Dornhaus (2011) predators were in effect cryptic (no spider models were used) and the colour difference between high- and low-reward flowers was highly salient. In contrast, in our study, discrimination of high- and low-reward flowers was very difficult, and in some groups predators were conspicuous, as they can be in the field (Defrize et al. 2010). At least at the patch level used in our experiments, it appears that the additional costs of detecting cryptic predators (Ings & Chittka 2008; Ings et al. 2012) are outweighed by the benefits of occasionally visiting a flower with over twice the energetic rewards of the safe flower type. Furthermore, the reduced cognitive demands of detecting conspicuous predators enable bees to continue to forage from risky but rewarding species.

In summary, our study clearly shows that bumblebees are able simultaneously to discriminate floral rewards based upon subtle visual differences (colour) and avoid cryptic predators, but will only do so when the benefits outweigh the costs. These findings highlight the importance of considering sensory processing and cognitive abilities of prey when modelling predator–prey interactions (Spaethe et al. 2006; Ings & Chittka 2008; Dukas 2009; Ings et al. 2012). Furthermore, our study contributes to the growing body of evidence showing the importance of trait-mediated indirect effects of predators (e.g. Gonçalves-Souza et al. 2008; Ings & Chittka 2009; Schoener & Spiller 2012). In particular we showed that the costs associated with detecting cryptic predators and discriminating similar floral colours could lead to strong trait-mediated effects on plants and may benefit mimic plant species that produce little or no floral rewards.

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APPENDIX. PRELIMINARY COLOUR DISCRIMINATION TEST

Methods

The aim of the test was to find two colours that are possible, but difficult for bees to distinguish. We chose two different shades of yellow (dark yellow and light yellow) whose distance in the bee colour hexagon (Chittka 1992) was 0.084 units. It is known that bees can easily discriminate between colours 0.152 hexagon units apart but find it impossible to differentiate colours less than 0.01 units apart (Dyer & Chittka 2004b). Therefore, bees should find it difficult, but not impossible to discriminate between our chosen colours. To test this we gave bees ($N=5$) a choice between rewarding dark yellow flowers (50% v/v sucrose) and distasteful light yellow flowers containing 0.12% quinine hemisulphate salt solution. A second control group of bees ($N=5$) from the same colony were exposed to dark yellow flowers (rewarded) and easily distinguishable white flowers (punished with quinine). Individual bees in both groups were allowed to make 200 flower choices to determine whether they could learn to distinguish rewarded and punished flower colours.

Results

All bees learnt that dark yellow flowers were rewarding as the proportion of dark yellow flowers chosen during the last 30 choices was significantly higher than that during the first 30 choices (paired t test: $t_4 = 2.91$, $P = 0.01$). This confirmed that bees were able to learn to distinguish the two shades of yellow despite their high degree of similarity (Fig. A2). Furthermore, the average

percentage of correct choices during the last 30 choices was significantly higher for the easily distinguishable colours (white and dark yellow flowers) than for the more similar colours (dark and light yellow) flowers (t test: $t_4 = 2.48$, $P = 0.03$). This confirmed that although bees are able to discriminate the two similar shades of yellow, they find the task significantly more challenging than the task in which the colours were highly discriminable.

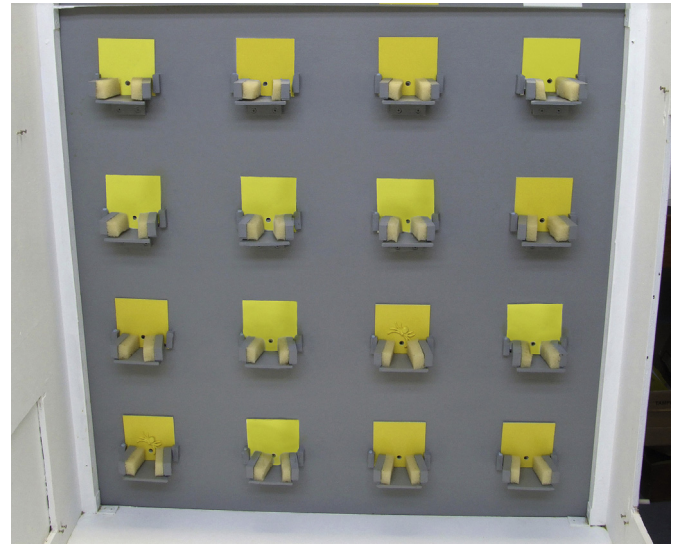


Figure A1. Experimental set-up demonstrating the artificial meadow containing two similar shades of yellow flowers while two (25%) of the highly rewarding flowers (dark yellow) harboured cryptic spiders. The positions of the flowers and spiders were randomly reshuffled for each foraging bout. The spiders were white in the conspicuous spider group.

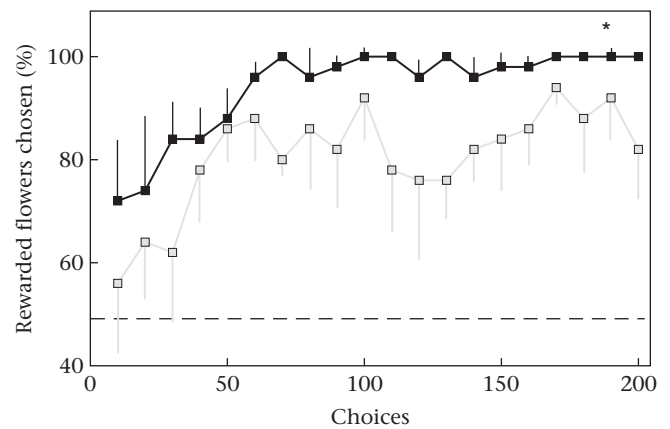


Figure A2. Discrimination test for similar and distinct colours. The black line is the mean \pm SEM percentage of bees choosing rewarded flowers between easily distinguishable colours (white versus dark yellow), and the grey line is between colours that were hard to distinguish (dark yellow versus light yellow). Each data point represents 10 choices.