Animal Behaviour xxx (2013) 1–8

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 8 March 2013
Initial acceptance 2 April 2013
Final acceptance 16 July 2013
Available online xxx
MS. number: 13-00212R

Keywords:
attention
bumblebee
Bombus terrestris
foraging
predator avoidance
predator crypsis
visual search

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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0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.07.029

Please cite this article in press as: Wang, M.-Y., et al., Can bees simultaneously engage in adaptive foraging behaviour and attend to cryptic predators?, Animal Behaviour (2013), http://dx.doi.org/10.1016/j.anbehav.2013.07.029

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

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