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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. Here we ask whether bees 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 both with cryptic and conspicuous spiders, finding that bees had no difficulty avoiding conspicuous spiders while still foraging adaptively. Conversely, they prioritised predator avoidance at the expense of maximising 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

46 difficult foraging tasks while simultaneously avoiding cryptic predators, but only do
47 so when avoidance of gustatory punishment justifies the increased costs.
48
49 keywords: attention, bumblebees, *Bombus terrestris*, foraging, predator avoidance,
50 predator crypsis, visual search
51

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, i.e. 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 which 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

70 flower they are hunting on (Morse 1986). They even preferentially hunt on high
71 quality flowers (Morse 1986), which are also preferred by foraging bees (Menzel et al.
72 1993; Heiling et al. 2004).

73 We have a good understanding of the individual problems facing foraging bees:
74 how they choose between different flowers (Giurfa & Lehrer 2001; Shafir et al. 2003;
75 Chittka and Raine 2006) and how they interact with predators (Heiling & Herberstein
76 2004; Dukas 2005; Reader et al. 2006). Bees can associate food rewards with specific
77 floral traits, such as colour, and can successfully discriminate between even subtle
78 differences in traits to maximise foraging efficiency (Dyer & Chittka 2004a).
79 Furthermore, bees are able to learn to avoid both individual flowers harbouring
80 predators and sets of flowers of a given type (colour) associated with predation risk
81 (Ings & Chittka 2008, 2009; Jones & Dornhaus 2011). However, it is not known how
82 bees perform when exposed to both flower colour discrimination and predator
83 avoidance tasks simultaneously, a situation which bees must naturally face. Evidence
84 from field studies suggests that bees may choose to avoid a patch harbouring
85 predatory crab spiders (Dukas & Morse 2003), and laboratory studies indicate that
86 bees may also choose to switch to a less risky flower species (Ings & Chittka 2009;

87 Jones & Dornhaus 2011). Therefore, we ask whether bees have the perceptual and
88 cognitive processing power to carry out such tasks simultaneously.
89 Early work on insects seemed to indicate that pollinators can only efficiently deal
90 with one task at a time (Lewis 1986), and indeed animals with substantially larger
91 brains have extensive capacity limitations in perceptual processing resulting in
92 significant costs associated with performing the precise discrimination of more than
93 one stimulus dimension (Kahneman 1973; Pashler 1998; Dukas 2009). For example,
94 in humans there are severe information processing consequences when one must
95 divide attention between two forms of visual input as simple as shape and orientation,
96 such that only one task can be attended to at a time (Joseph et al. 1997). Therefore, we
97 might expect such capacity limitations to be all the more important in much smaller
98 animals with concomitant smaller nervous systems, such as bumblebees.
99 In this study we ask whether bumblebees are able to maximise energy gains by
100 solving a difficult colour discrimination task whilst simultaneously exposed to
101 predation threat from camouflaged or conspicuous predators. Firstly, we exposed bees
102 to an ecologically relevant scenario where they foraged in an artificial meadow with
103 two visually similar flower types differing in reward quality. Visiting the highly
104 rewarding flower type was risky because 25% of flowers harboured predatory crab

spider models. If bees are able to simultaneously solve colour discrimination and predator avoidance tasks we predict that they will 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 i) bees will prioritise predator detection and avoidance when predators are camouflaged and ii) they will continue to maximise energy gains when predators are highly conspicuous. Secondly, because bees did not simultaneously focus on predator avoidance and maximising energy gains we ask 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 predict that bees will be unable to focus on predator avoidance as well as discriminating between rewarding and distasteful flowers. Ultimately, we hypothesise that such limitations in sensory processing will increase indirect trait-mediated effects of predators on plants when predators are cryptic – i.e. bees will alter their foraging preferences when exposed to predation threat from camouflaged predators.

METHODS

Study Animals

123 Three colonies of bumblebees (*Bombus terrestris* Dalla Torre 1882) from a
124 commercial supplier (Syngenta Bioline Bees, Weert, Netherlands) were used in the
125 experiment. All the bees were individually tagged with number tags (Christian Graze
126 KG, Weinstadt-Endersbach, Germany). Colonies were kept at room temperature
127 (~23°C) and subjected to a 12 hr light/dark cycle (light on at 8am). Sucrose solution
128 (50%, v/v) and pollen was provided ad libitum. A total of 54 foragers were used in the
129 experiments.

130

131 *Experimental Apparatus*

132 All experiments were conducted in a wooden flight arena (1.0 × 0.72 × 0.73
133 m) with a UV-transmitting Plexiglas lid. Two twin lamps (TMS 24 F with HF-B 236
134 TLD [4.3 kHz] ballasts, Philips, The Netherlands) fitted with Activa daylight
135 fluorescent tubes (Osram, Germany) were suspended above the flight arena to provide
136 controlled illumination. Artificial flowers (7×7 cm acrylic, 1 mm thick) were arranged
137 in a four by four vertical grid on one end wall of the arena on a grey background (Fig.
138 A1). The opposite wall contained an entrance hole through which the bees could enter
139 the arena from the colony. Bees were able to access rewards (sucrose solution)
140 through a hole which was 10 mm above a wooden landing platform (40×60 mm). A

141 constant flow (1.85 ± 0.3 µl per minute) of sugar solution (reward) was supplied to
142 each flower from individual syringes attached to two multi-syringe infusion pumps
143 (KD Scientific, KD220, Holliston, USA). At each flower, the solution was delivered
144 via silicone tubing ending in a 26G syringe needle (BD Microlance Drogheda, Ireland;
145 0.45 × 13 mm) temporarily held in place in front of the hole in the wall by reusable
146 adhesive (Blue Tack ®, Bostick, USA). A maximum droplet volume of 4.70 + 0.3 µl
147 could be reached before it fell into a 'waste pot' which was not accessible to bees
148 (thus mimicking a flower that had been emptied by a bee). This avoided unvisited
149 flowers from becoming excessively rewarding and the slow refill rate prevented bees
150 from revisiting a flower immediately after removing the reward. Re-visits did occur
151 (3.59 ± 0.4 per flower) as we had a limited number of flowers in the arena, but these
152 typically occurred after the bees had visited several other flowers in the arena first
153 (130.84 ± 14.7 seconds between revisits). Robotic 'spider arms' (custom-built by
154 Liversidge & Atkinson, Romford, UK) covered with sponges were set up at the base
155 of the flowers to simulate predation attempts. The trapping mechanism enabled us to
156 capture bees without causing physical damage. 'Dangerous flowers' were fitted with
157 life-sized crab spider (*Misumena vatia*) models (l = 12mm, made from Gedeo Crystal
158 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 per second using two video cameras connected to a computer running Trackit 3D software (BIOBSERVE GmbH, Bonn, Germany).

Pre-training

All bees were allowed to fly in the flight arena without any presentation of floral signals for at least one day before the experiment. A constant flow (1.85 + 0.3 µl per minute) 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 to simultaneously solve a colour discrimination task to maximise

175 energy gains whilst avoiding conspicuous or camouflaged predators. Bees could
176 choose between two types of flowers that were similar shades of yellow to human
177 observers (neither shade of yellow reflected appreciable amounts of UV light and
178 therefore both colours were green to bees, i.e. they stimulated predominantly the bees'
179 green receptors; Fig. 1a). The flower colours were chosen so that bees could
180 distinguish between them, but only with significant difficulty (see Supplementary
181 Data). The darker shade of yellow (which was associated with high quality rewards)
182 was distinguished from the lighter yellow shade (low quality rewards or penalties) by
183 a colour hexagon difference of only 0.084 units, which indicates poor discriminability
184 according to previous work (Dyer & Chittka 2004a). We also tested experimentally
185 that the two colours were distinguishable for bees, but with difficulty (Appendix 1).

186 The high quality (dark yellow) flowers carried a risk of predation from either
187 conspicuous or cryptic 'robotic spiders' (Ings & Chittka 2008). Twenty-five percent
188 of the flowers harboured a spider. Conspicuous spiders were of white appearance to
189 human observers. They absorbed UV to some extent (Fig. 1b), and they therefore
190 appear blue-green to bees. However, some of the white spiders' reflectance still
191 extended into the highly sensitive UV-receptor's domain below 400nm. These spiders'
192 colour loci therefore appear very close to the uncoloured point ('bee-white', in the

193 centre of the colour hexagon; Fig. 1a). They were distinguished by a colour contrast
194 (colour hexagon distance) of 0.439 units from the dark yellow flower substrate,
195 indicating a high level of conspicuousness. The contrast provided specifically to
196 bumblebees' green receptor is also important, since this receptor feeds into the
197 motion-sensitive system and is thus often crucial in target detection (Dyer et al. 2008).
198 Green receptor contrast between white spiders and their dark yellow flower backdrop
199 is likewise large (0.104 on a scale of 0 to 1 where zero equals no contrast) indicating
200 high detectability of the white spiders both in terms of colour contrast as well as green
201 contrast. Conversely, cryptic spiders were dark yellow like the flowers on which they
202 were placed, and both colour contrast (0.036 hexagon units) and green contrast (0.004)
203 values were very low, indicating poor detectability of these spiders. As in a previous
204 study (Ings & Chittka 2008) the spiders were only detectable using
205 shape-from-shading cues.

206 Individual bees (N = 34 randomly selected from 2 colonies) were initially
207 trained to distinguish between the shades of yellow, with the darker yellow flowers
208 containing high quality rewards (50% v/v sucrose) and the lighter yellow flowers
209 providing low quality rewards (20% v/v sucrose). Training continued until bees made
210 a minimum of 200 flower choices. To reach this criterion, bees returned to the nest to

empty their crops three to five times (number of foraging bouts: cryptic = 4.9 ± 0.7; conspicuous = 3.7 ± 0.3, total duration in minutes: cryptic = 45.27 ± 3.71; conspicuous = 40.93 ± 3.43). 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 five minutes, 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 (total duration of avoidance training in minutes: cryptic = 32.52 ± 2.91; conspicuous = 41.32 ± 5.09). 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

229 spider for two seconds. This emulates natural spider attacks on bumblebees where
230 bees are grasped by the raptorial forelegs of the spider but manage to escape, avoiding
231 immobilization by the spider's bite. As in colour discrimination training, locations of
232 all flowers were randomly reassigned between foraging bouts (number of foraging
233 bouts: cryptic = 4.9 ± 0.8; conspicuous = 4.2 ± 0.3).

234

235 *Experiment 2: Discriminating Gustatory Punishment and Reward under Predation*
236 *Risk*

237 To determine whether the apparent inability of bees to solve colour
238 discrimination and cryptic predator avoidance tasks simultaneously was due to
239 limitations in sensory processing or attention we conducted a second experiment
240 where the balance of risk and reward was adjusted beyond that naturally encountered.
241 In this experiment, a third group of bees (N = 10 from colony 3) was given an
242 additional incentive to discriminate between the shades of yellow flower by replacing
243 the low quality rewards with a form a gustatory punishment, a distasteful (bitter)
244 quinine hemisulfate solution that bees rapidly learn to avoid (Chittka et al. 2003). This
245 solution contained no sucrose. Bees do not ingest this solution and abort flower visits
246 immediately upon tasting it. It has been demonstrated empirically that such

247 punishment generates much stronger discrimination than simply rewardless flowers
248 that need to be distinguished from rewarding flowers (Chittka et al. 2003). Thus, bees
249 were initially trained to distinguish between dark yellow rewarding flowers containing
250 50% v/v sucrose solution and light yellow distasteful flowers containing 0.12%
251 quinine solution. After colour discrimination training for 200 flower choices (see
252 Experiment 1, total duration in minutes = 37.79 ± 3.78) bees were then exposed to
253 predation risk (25%) from cryptic spiders (the hardest predator avoidance task) on the
254 rewarding (dark yellow) flowers for a further 200 flower visits (total duration = 31.75
255 ± 2.33 minutes). Locations of flowers were randomly re-assigned between every
256 foraging bout (number of bouts: colour discrimination training = 3.7 ± 0.3; predator
257 avoidance training = 4.4 ± 0.4).

258

259 *Data Analysis*

260 Individual bees' preferences for highly rewarding flowers (dark yellow) were
261 calculated from their final 30 flower choices of the colour discrimination training
262 phase in both experiments. These preferences were then used to determine predator
263 avoidance during the training phase, where bees were exposed to predation risk
264 (pairwise comparisons using paired *t* tests or Wilcoxon Signed Rank Tests if data

violated the assumptions of the *t* test – all tests were 2-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 (2 dangerous flowers out of 8 highly rewarding flowers) with a probability of 0.8 x 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 (length) by 9 cm (width) by 9 cm (height) from 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 whilst 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) and JMP (v. 7, SAS Institute). Four bees which lost motivation (i.e. stopped foraging) during training were excluded from the analysis (2 per group in Experiment 1).

283

284 # RESULTS

285 *Discrimination Learning*

286 Bees in both experiments were trained to differentiate between two similar
287 shades of yellow flower. In the first experiment, colour discrimination was reinforced
288 by differences in reward quality, whereas in the second experiment it was reinforced
289 by the use of a gustatory punishment in the lighter shade of flowers versus sugar
290 reward in the dark yellow flowers. All bees commenced training without a preference
291 (Fig. 2) for either shade of yellow, irrespective of reward level or punishment (mean
292 [± 1SEM] percentage of dark yellow flowers selected during the first 30 choices:
293 conspicuous spider group = 50.0 ± 2.25, cryptic spider group = 48.7 ± 5.4, quinine
294 group = 49.3 ± 3.9; ANOVA: $F_{2,37} = 0.029$, $P = 0.971$; one sample *t* test against
295 random visits [50%] on pooled data for all groups of bees: $t_{39} = -0.285$, $P = 0.777$; Fig.
296 2). However, by the end of the colour discrimination training, bees in Experiment 1
297 had developed a slight, but significant preference (Fig. 2) for the dark yellow flowers
298 (59.7 ± 2.0 % [pooled data for both groups] dark yellow flowers selected during the
299 last 30 choices; one sample *t* test [against 50%]: $t_{29} = 4.853$, $P < 0.001$). Furthermore,
300 colour discrimination was significantly greater in Experiment 2 where bees were

301 incentivised by bitter quinine in the light yellow flowers (83.3 ± 4.0 % dark yellow
302 flowers selected: *t* test [Experiment 1 versus Experiment 2], t_{38} = -5.710, $P < 0.001$;
303 Fig 2).

304

305 *Discriminating Reward Quality under Predation Risk*

306 Both groups of bees in Experiment 1 rapidly learnt to avoid robotic spiders (Fig. 3),
307 although the initial avoidance response was stronger when spiders were conspicuous
308 (Fig. 3; Mann-Whitney *U* Test: $U = 197.5$, $N_1 = N_2 = 15$, $P < 0.001$). By the end of
309 training, both groups visited virtually no dangerous flowers (median percentage
310 during the last 30 choices for both groups = 0.0 and the inter-quartile range = 3.3;
311 Wilcoxon Signed Rank Test: $T = 4.790$, $N = 30$, $P < 0.001$; Fig. 3). However, the two
312 groups differed significantly in their ability to simultaneously discriminate between
313 similar shades of yellow flowers in order to maximise their energy intake (mean
314 percentage of safe, highly rewarding flowers chosen during the last 30 choices:
315 cryptic spiders = 36.7 ± 2.8, conspicuous spiders = 52.7 ± 4.4; *t* test: $t_{28} = 3.097$, $P =$
316 0.004; Fig. 2). Bees encountering conspicuous spiders regained their slight preference
317 for high reward flowers (one sample *t* test against random visits [37.5 %]: $t_{14} = 3.483$,
318 $P = 0.004$) 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).

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 to simultaneously 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 inter-quartile range = 3.3; Wilcoxon Signed Rank Test: T = 2.805, N = 10, P = 0.005; Fig. 3). Furthermore, they were able to simultaneously maintain their high level of colour discrimination (mean 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 maximise energy intake by using subtle differences in flower colour to differentiate between reward quality. The second was to detect and avoid predators that were either conspicuous or cryptic. We found that when predator detection was difficult, bees prioritised 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 prioritisation 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 – i.e. 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 focus attention on flowers that match 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 training (Fig. 3). It is therefore likely that safe (plain) dark yellow flowers are processed as targets

371 and light yellow flowers and dangerous flowers are processed as distractors. In this
372 case bees would only need to compare each flower against one search image and
373 therefore attend to only a single visual search task.

374 A different pattern emerged when spiders were cryptic. Due to lack of contrast
375 between spiders and background flowers (Fig. 1) we would expect bees to initially
376 view dangerous flowers as desirable target flowers. Indeed, this is exactly what was
377 observed during the first few choices made by bees in the cryptic spider group that
378 chose significantly more dangerous flowers than bees in the conspicuous spider group
379 during their first 30 choices (Fig. 3). Despite this, bees exposed to cryptic spiders did
380 learn to avoid dangerous flowers, indicating that they had developed a new search
381 image for cryptic spiders (Ings et al. 2012). Therefore, we are led to ask how bees
382 process each flower during visual search. Avoiding dangerous flowers and
383 maximising energy gains would require a two-step process due to the similarity
384 between target and distractor flowers: bees could either assess flowers as
385 spider-infested or spider-free and then discriminate between flower colours, or *vice*
386 *versa*. This sequential decision making could make the assessment more costly in
387 terms of time than the one step process necessary for avoiding conspicuous spiders
388 (Spaethe et al. 2006; Ings et al. 2008). Our results showed that bees encountering

389 cryptic spiders prioritised predator avoidance at the expense of discriminating floral
390 reward quality of the remaining safe flowers. To understand whether this failure to
391 attend to both tasks is due to principal limitations in sensory processing and cognitive
392 abilities (Lewis 1986; Dukas 2009) we need to consider how bees responded to
393 predation threat in Experiment 2 when they were strongly incentivised to discriminate
394 between the similar shades of yellow.
395 When one flower colour was associated with a positive value (sucrose reward)
396 and the other with a negative value (quinine), bees were able to maintain two
397 value-defined categories for the task (light yellow = punishment, dark yellow =
398 reward). As a result, discrimination between light and dark yellow flowers was
399 substantially better than in Experiment 1 (Fig. 2). Furthermore, bees also maintained
400 this high level of discrimination under predation threat from cryptic spiders on the
401 rewarding flowers. This difference in response compared to bees in the cryptic spider
402 group in Experiment 1 shows that bees are able to simultaneously solve both complex
403 visual search tasks given sufficient incentive. However, this incurs elevated temporal
404 costs which indicate a sequential assessment of the flowers for safety (spider
405 presence/absence) and reward level (by colour), as predicted by assuming that
406 bumblebee are using restricted parallel visual search (Morawetz & Spaethe 2012;

407 Spaethe et al. 2006). Therefore, we are led to conclude that bees are able to divide
408 their attention between two complex visual search tasks in two different contexts. This
409 result is all the more remarkable given the failures of divided attention in related tasks
410 in birds (Dukas & Kamil 2000) and humans (Joseph et al. 1997).

411 An alternative explanation to divided attention is that bees categorised
412 (Srinivassan 2010; Avargues-Weber et al. 2012a) flowers into “good” or “bad” types,
413 irrespective of whether penalties were predation attempts or of a gustatory nature.
414 Light yellow flowers, which contain quinine in Experiment 2, could be classed as
415 poor foraging options, as could dark yellow flowers harbouring cryptic spiders. Dark
416 yellow flowers without spiders could be classed as desirable foraging options. Thus,
417 one might assume that a bee only needs to follow a simple rule – i.e. if the flower
418 matches the search image for ‘good’ then visit, otherwise avoid. However, the
419 increased inspection times in the face of two undesirable types of flowers indicate that
420 bees actively discriminate against both types of ‘bad’ flowers, i.e. a scenario based on
421 visual target categorisation would still require the memorisation of three search
422 images being employed simultaneously.

423 Finally, our results have interesting implications for the temporal costs of decision
424 making under natural conditions. Why did bees under predation threat choose not to

425 engage in efficient foraging when solving the colour discrimination task would have
426 meant feeding from flowers bearing more than twice the energetic rewards? In
427 Experiment 2 bees had to spend a significantly (~28%) longer time inspecting flowers
428 under predation threat from cryptic spiders (Fig. 4). Inspection of flowers is carried
429 out in flight, which is an energetically demanding activity (Kacelnik et al. 1986;
430 Hedenström et al. 2001), so even small increases in inspection times are likely to bear
431 high energetic costs to bees. The increased inspection times observed in Experiment 2
432 can largely be attributed to the detection and avoidance of cryptic spiders (Ings &
433 Chittka 2008; Ings et al. 2012) which can lead bees to shift to alternative safe flower
434 types if they are as rewarding as risky flowers (Ings & Chittka 2009). Furthermore,
435 theoretical models (Jones 2010) predict that bees can maximise lifetime foraging
436 gains by switching to lower quality flowers when highly rewarding flowers have a
437 higher level of predation risk. Indeed, bumblebees do appear to make optimal choices
438 under laboratory conditions when predation risk is simulated (Jones & Dornhaus
439 2011), although field studies on honeybees show that they are less inclined to avoid
440 risky but highly rewarding patches (Llandres & Rodríguez-Gironés 2011). While
441 these differences could represent species specific responses, they are equally likely to
442 be due to differences in the balance of risk and reward as well as the difficulty of the

443 visual search tasks involved. In the study by Jones and Dornhaus (2011) predators
444 were in effect cryptic (no spider models were used) and the colour difference between
445 high and low reward flowers was highly salient. In contrast, in our study,
446 discrimination of high and low reward flowers was very difficult, and in some groups
447 predators were conspicuous, as they can be in the field (Defrize et al. 2010). At least
448 at the patch level used in our experiments, it appears that the additional costs of
449 detecting cryptic predators (Ings & Chittka 2008; Ings et al. 2012) are outweighed by
450 the benefits of occasionally visiting a flower with over twice the energetic rewards of
451 the safe flower type. Furthermore, the reduced cognitive demands of detecting
452 conspicuous predators enable bees to continue to forage from risky but rewarding
453 species.

454 In summary, our study clearly shows that bumblebees are able to simultaneously
455 discriminate floral rewards based upon subtle visual differences (colour) and avoid
456 cryptic predators, but will only do so when the benefits outweigh the costs. These
457 findings highlight the importance of considering sensory processing and cognitive
458 abilities of prey when modelling predator-prey interactions (Spaethe et al. 2006;
459 Dukas 2009; Ings & Chittka 2008; Ings et al. 2012). Furthermore, our study
460 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 et al. 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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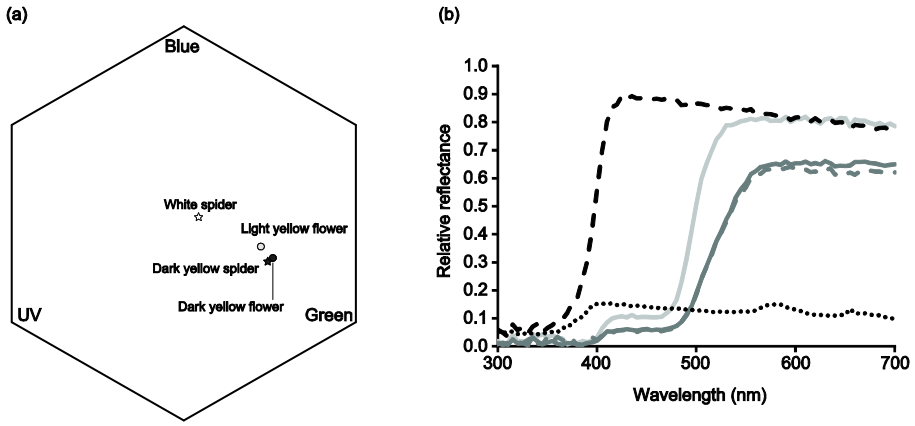
598 FIGURES AND FIGURE LEGENDS

Figure 1

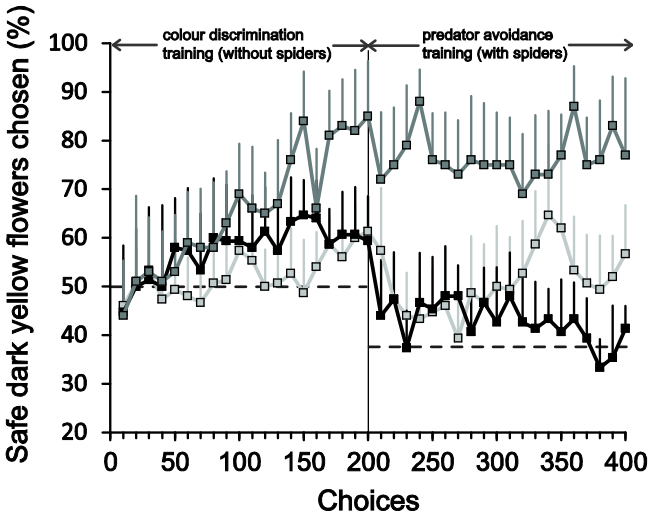


599

600 **Fig. 1. (**a) Appearance of yellow flowers (circles: light grey for light yellow and dark
601 grey for dark yellow) and spiders (stars: white for conspicuous spiders and dark grey
602 for cryptic spiders) in bee colour space (calculated using *Bombus terrestris* colour
603 receptor sensitivity functions in Skorupski et al. 2007) relative to the grey background
604 colour (centre of the hexagon). Positions of the colour loci in the hexagon indicate
605 excitation differences of the three bee colour receptors. The corners of hexagon
606 labelled UV, Blue and Green correspond to hypothetical maximum excitation of one
607 receptor combined with zero excitation in the two others. The angular position in the
608 hexagon (as measured from the centre) is indicative of bee subjective hue. Loci that
609 are close together appear similar to bees and loci that are far apart appear different. (b)

610 Spectral reflectance curves of artificial flowers, spiders and the grey background of
611 the meadow. The dashed lines represent spiders (dark grey = dark yellow spiders and
612 light grey = white spiders), solid lines flowers (dark grey = dark yellow flowers and
613 light grey = light yellow flowers) and the dotted line represents the grey meadow
614 background.

Figure 2



615

616 **Fig. 2.** The mean (plus upper 95% CI) percentage of safe high reward flowers
617 (without spiders) chosen during consecutive blocks of 10 trials during colour
618 discrimination and predator avoidance training in Experiments 1 & 2. Black
619 represents bees exposed to cryptic spiders and light grey bees exposed to conspicuous
620 spiders in Experiment 1, while dark grey represents bees in Experiment 2 that were
621 exposed to cryptic spiders and quinine punishment in distractor flowers. The dashed

lines represent the expected percentage of high reward flowers if bees foraged completely at random, i.e. with no preference for either flower type.

Figure 3

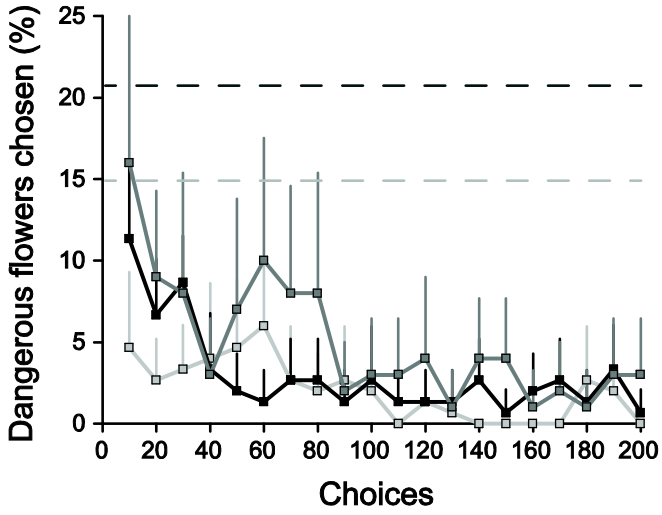
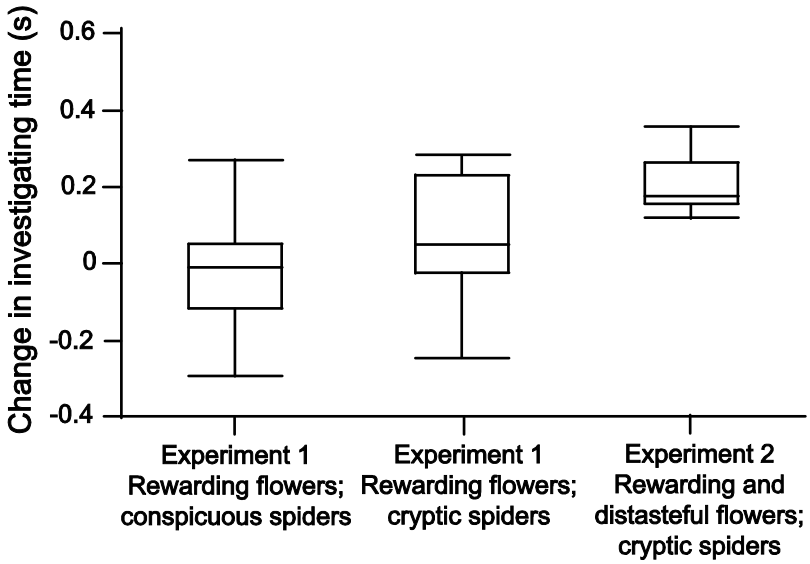


Fig. 3. The mean (plus upper 95% CI) percentage of dangerous flowers chosen during consecutive blocks of 10 trials during avoidance training in Experiments 1 and 2. Black represents bees exposed to cryptic spiders and light grey bees exposed to conspicuous spiders in Experiment 1, while dark grey represents bees in Experiment 2 that were exposed to cryptic spiders and quinine punishment in distractor flowers. The dashed lines represents the avoidance thresholds (percentage of dangerous flowers expected 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.

634

Figure 4



635

636 **Fig. 4**. Difference in floral investigation time between colour discrimination training

637 and predator avoidance training (average investigating time per flower after adding

638 spiders minus average time before adding spiders).

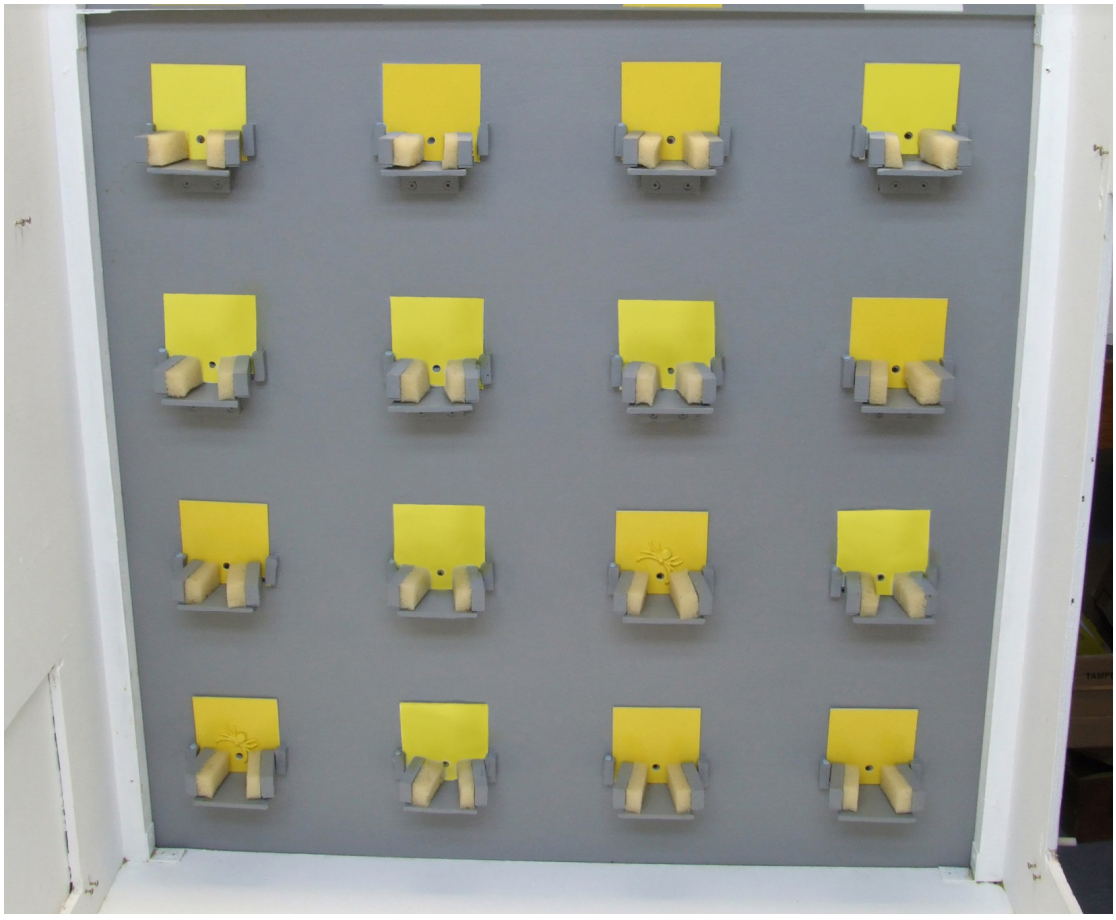


Fig. A1. Experimental setup demonstrating the artificial meadow containing two similar shades of yellow flowers while two (25%) of the highly rewarding flowers (dark yellow) harboured cryptic spiders. The positions of the flowers and spiders were randomly reshuffled for each foraging bout. The spiders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

Figure A2

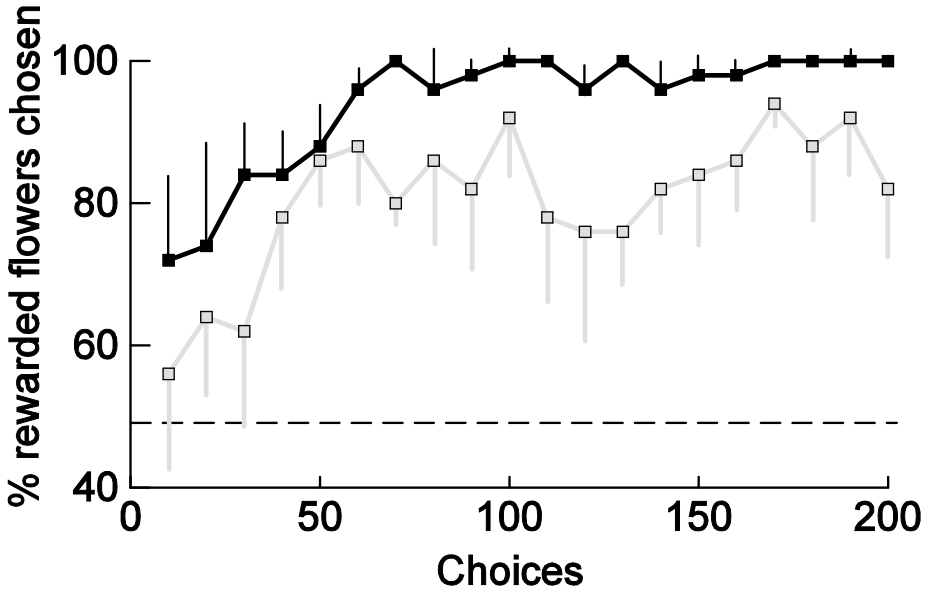


Fig A2. Discrimination test for similar and distinct colours. The black line is the average (+/- 1SEM) percentage of bees choosing rewarded flowers between easily distinguishable colours (white v. s. dark yellow), and the grey line is between colours that were hard distinguish (dark yellow v. s. light yellow). Each data point represents 10 choices.

APPENDIX 1: EXPERIMENTAL PROCEDURES AND RESULTS FOR THE PRELIMINARY COLOUR DISCRIMINATION TEST.

METHODS

The aim of the test was to find two colours which are possible, but difficult for bees to distinguish. We chose two different shades of yellow (dark yellow & 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 hemisulfate 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 where the colours where highly discriminable.