

2 **Getting to the start line: how bumblebees and honeybees are**
3 **visually guided towards their first floral contact**

4 L. L. Orbán · C. M. S. Plowright

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7 **Abstract** Much of the literature on foraging behaviour in
8 bees focuses on what they learn after they have had
9 rewarded experience with flowers. This review focuses on
10 how honeybees and bumblebees are drawn to candidate
11 food sources in the first place: the foundation on which
12 **AQ1** learning is built. Prior to rewarded foraging experience,
13 flower-naïve bumblebees and honeybees rely heavily on
14 visual cues to discover their first flower. This review lists
15 methodological issues that surround the study of flower-
16 naïve behaviour and describes technological advances. The
17 **AQ2** role of distinct visual properties of flowers in attracting bees
18 is considered: colour, floral size, patterning and social cues.
19 The research reviewed is multi-disciplinary and takes the
20 perspectives of both the bees and the plants they visit.
21 Several avenues for future research are proposed.

22
23 **Keywords** Visual recognition · Bumblebees ·
24 Honeybees · Innate · Unlearned behaviour · Flower-naïve
25

26 **Introduction**

27 How do bees first find flowers? To behavioural ecologists,
28 the question itself may seem perplexing: finding flowers is
29 just what bees do. That bees are well designed to exploit
30 floral resources is so self-evident that at first glance it may
31 seem as if there is nothing to explain. Indeed, much of the

research on foraging behaviour concerns what bees do, and 32
how they do it, after they have had their first rewarded 33
experience on flowers (see reviews by Gould, 1990; Bit- 34
terman, 1996; Chittka and Thomson, 2001; Menzel, 2001; 35
Raine et al., 2006; Benard et al., 2006; Giurfa, 2007; Dukas, 36
2008; Goulson, 2010; Avarguès-Weber et al., 2011; Dyer, 37
2012). There is comparatively less research on what they do 38
before: when workers leave their colony for the first time, 39
having never yet encountered a flower, how do they identify 40
candidate food sources? This review is centred on how bees 41
are directed to their first floral contact where pollen and 42
nectar rewards begin to shape their motor responses into 43
efficient food-directed behavioural sequences: how bees get 44
to the start line of their foraging careers. 45

If workers in eusocial species fail to find food, especially 46
at the beginning of colony cycle, not only are a few indi- 47
viduals placed at risk, but the whole colony could fail to 48
thrive or die out altogether. This review focuses on hon- 49
eybees (*Apis* spp. L., 1758) and bumblebees (*Bombus* spp. 50
Latreille, 1802). They are central place foragers that con- 51
tribute to the nutrition of the entire colony. In addition, the 52
visual processing in these Hymenoptera has been excep- 53
tionally well documented (Dyer, 2012)—there is a 54
substantial body of literature to use in eventual comparisons 55
in future research between behaviours before and after the 56
first floral reward. 57

The question of what draws bees to potential sources of 58
nectar and pollen may be of interest not only to insect be- 59
haviourists but also to pollination ecologists: this paper 60
approaches the problem from the perspectives of the prob- 61
lems faced by insects and those faced by the plants they 62
visit. Plants “advertise” themselves (Dafni et al., 2005) and 63
incur high costs in doing so (Primack and Hall, 1990) but 64
are, nonetheless, frequently subject to pollination deficits. 65
Growers of insect-pollinated field crops such as blueberries 66

A1 L. L. Orbán · C. M. S. Plowright
A2 School of Psychology, University of Ottawa, Ottawa, Canada

A3 *Present Address:*
A4 L. L. Orbán (✉)
A5 Department of Psychology, Kwantlen Polytechnic University,
A6 12666 72nd Avenue, Surrey, BC, Canada
A7 e-mail: lorban@uottawa.ca

67 and cranberries routinely pay for commercial pollination
68 services to improve crop quality and yield (Free, 1993;
69 Velthuis and van Doorn, 2005). Given the worldwide
70 declines in bumblebees (Goulson et al., 2008; Williams and
71 Osborne, 2009), the competition amongst flower species to
72 attract pollinators may be on the rise. As noted by Buch-
73 mann and Nabhan (1996, p. 258): “Fewer pollinators
74 ultimately mean fewer plants”, and understanding their
75 pollination ecology will be critical to protect them from
76 extinction.

77 The terminology regarding our subject area is fraught
78 with difficulties in interpretation. The term “innate” (or a
79 synonym, “instinctive”), though it persists in the biological
80 literature, is problematic (Bateson, 1984; Oyama, 2000;
81 Scholz, 2002; Bateson and Mamei, 2007; Mamei and
82 Bateson, 2006, 2011) because it can take on several non-
83 interchangeable meanings (e.g. adaptive, unmodifiable,
84 inborn, hardwired, unlearned, species-specific, etc.). What
85 is worse, evidence for one meaning can too easily be mis-
86 taken as entailing evidence for the other (Bateson and
87 Gluckman, 2011). One possible solution is to use the term
88 “pre-functional” (Hogan, 1994)—in our case, the behaviour
89 that occurs prior to functional experience with flowers. A
90 similar tack is to characterize the bees themselves as
91 “flower-naïve” (Giurfa et al., 1995) or “foraging-naïve”
92 (Milet-Pinheiro et al., 2012). We will adopt these expres-
93 sions because they have the advantage that they avoid any
94 implication that no experience whatsoever is necessary for
95 the development of behaviour.

96 This review focuses only on visual cues that are attractive
97 to flower-naïve honeybees and bumblebees though in nat-
98 ure, odour cues are almost certainly important as well. In
99 bumblebees, workers take advantage of floral odours that
100 are brought into the colony by others (Dornhaus and Chit-
101 tka, 1999). The role of odour cues in isolation of, and in
102 combination with, visual cues has been documented for
103 solitary bee species (*Chelostoma rapunculi* Lepeletier,
104 1841): the relative importance of these cues changes with
105 experience (Milet-Pinheiro et al., 2012). The use of various
106 cues also depends on availability: bumblebees (*Bombus*
107 *impatiens* Cresson, 1863) can forage in complete darkness
108 (Chittka et al., 1994). The olfactory preferences of honey-
109 bees are reviewed by Riffell (2011). The chemical ecology
110 and evolution of bee–flower interactions are reviewed by
111 Dötterl and Vereecken (2010). Multi-sensory integration in
112 bees is reviewed by Leonard and Masek (2014).

113 The overriding question in this paper is not new. It can be
114 traced to the writings of Manning (1956, p. 198) (...“it is
115 necessary for a plant to attract bees in the first place, before
116 they are ‘aware’ of the food supply...”) and Free and Butler
117 (1959, p. 106) (“Little work has been done to discover those
118 features of flowers to which bees react on their very first
119 foraging flights, and such an investigation would be well

worth undertaking”). Giurfa et al. (1995) trace the question
back to none other than Charles Darwin (1876). What is new
is that now there are some answers. We begin with meth-
odological considerations, follow with an examination of
the role of various visual cues that have been investigated
and conclude with suggestions for future research. We draw
on the literature from perception, neuroscience, ecology and
computational science. The benefits of a multi-disciplinary
approach that integrates functional questions from biology
with mechanistic questions from psychology have been
delineated by Dukas (1998, 2004), Chittka and Thomson
(2001), Dukas and Ratcliffe (2009) and Shettleworth
(2010).

Methodological issues

Though bees can be tracked in the field over long distances
using harmonic radar (Osborne et al., 1999), it remains, as
noted by Lunau and Maier (1995), methodologically
intractable to determine the first flower choice of bees that
are known to be flower-naïve. Accordingly, most of the
research is conducted in the lab where the history of indi-
vidual workers is known and the floral options can be
controlled. Below we describe some of the standard pro-
cedures that have been used to investigate floral preferences
of flower-naïve bees and highlight some of the methodo-
logical pitfalls. This section is intended as a guide to
navigating the literature and as a list of experimental design
considerations for use in future research.

Pre-training

Workers that have had foraging experience in the lab typi-
cally fly directly to the source of food and return reliably. In
contrast, the flight paths of flower-naïve bumblebees are
typically meandering and it can take hours and even days
before they alight on any artificial patterns. Indeed, on their
first flights, the task of learning landmarks and the charac-
teristics of their nest entrance (Hempel de Ibarra et al.,
2009) may possibly take precedence over foraging. Even in
greenhouses where there is little else but rows of tomato
flowers, bumblebees can take 2–4 days before foraging
reliably on the flowers (Asada and Ono, 1996). In a flight
cage in our lab, the times in between first leaving a colony
and landing on one of two artificial flowers for a sample of
almost 200 bumblebees were distributed with a mode of
within 1 day, but a median of 11 days (Orbán, 2013, unpubl.
data). To circumvent this problem, bees are sometimes
trained to ostensibly neutral patterns such as black discs,
white discs (Rodríguez et al., 2004) or checkerboards
(Lehrer et al., 1995) and subsequently tested for their
preferences of new unrewarded patterns. This practice may

168 be innocuous when studying colour preferences: bees do not
 169 generalize their experience from pre-training with one col-
 170 our to testing on others, as long as the colours seem very
 171 different to them (Gumbert, 2000). Nonetheless, explicit
 172 tests of the effects of pre-training on subsequent pattern
 173 choice have shown differences in the behaviour of untrained
 174 (flower-naïve) and pre-trained (not-so-naïve) bumblebees
 175 (Séguin and Plowright, 2008; Plowright et al., 2011).
 176 Hence, the untested assumption that pre-training is neutral
 177 or unrelated to the test of floral preferences is tenuous.

178 Choices

179 Strictly speaking, a bee is flower-naïve for its first choice,
 180 but not for its second. It is an empirical matter, however,
 181 whether the first few unrewarded choices differ from the
 182 first. There is habituation of unlearned preferences: prefer-
 183 ences wane between testing sessions in the face of repeated
 184 exposure to patterns that offer no reward (Simonds and
 185 Plowright, 2004), but resurface again after time (Plowright
 186 et al., 2006). Over periods of prolonged testing on unre-
 187 warding patterns, where bees are free to return to and from
 188 the flight cage and their colony, increases and decreases in
 189 preferences oscillate (Orbán and Plowright, 2013). Within a
 190 testing session consisting of a series of unrewarded choices
 191 made upon the first trip away from the colony, however, we
 192 have found little or no change within short sessions of 16–20
 193 choices (Plowright et al., 2011, 2013).

194 One issue that remains unresolved is the effect of the
 195 number of floral options presented. Even with a single
 196 flower, there is a choice to accept or reject it. With two
 197 flowers, an apparent preference for one flower can be the
 198 result of an avoidance of the other: preferences are relative.
 199 Offering three options would further complicate the situa-
 200 tion. In the animal behaviour literature, the preference of
 201 one stimulus over the other can be affected in non-trivial
 202 ways by the introduction of a third option (Bateson, 2004).
 203 That this may be a real concern in our area is suggested by
 204 the work of Shafir (1994) who demonstrated intransitive
 205 preferences in honeybees (*Apis mellifera* L., 1758): in a
 206 series of binary choices that varied in the depth and volume
 207 of sucrose-water delivered, honeybees preferred A to B, B
 208 to C, C to D, but D to A.

209 Measures of preference

210 Choice behaviour can be measured in multiple ways, dif-
 211 fering in the level of apparent commitment to a floral
 212 stimulus by the bee: approach within a specified distance
 213 (e.g. 2 cm; Goulson et al., 2007); entering a corridor, in
 214 which a pattern is contained, in a maze (Simonds and Plo-
 215 wright, 2004; Séguin and Plowright, 2008); antennal contact
 216 with a test pattern (Pohl et al., 2008; Lunau et al., 2009)—

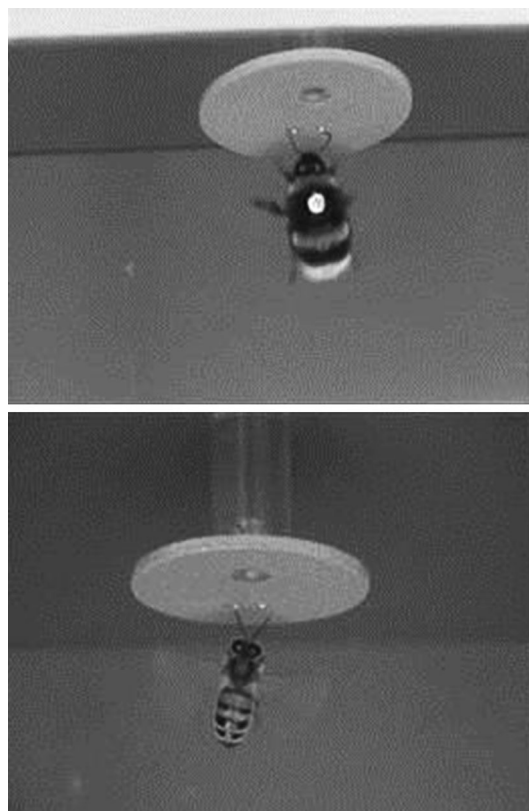


Fig. 1 Antennal reactions towards floral guides (*two dots*) by *Bombus terrestris* (above) and *Apis mellifera* (below). Photograph from Lunau et al. (2009). Reprinted with kind permission from Springer Science and Business Media

see Fig. 1 for an illustration with honeybees and bumble- 217
 bees; landing on a test pattern (Leonard and Papaj, 2011); 218
 floral exploration as defined by walking into an artificial 219
 flower (Orbán and Plowright, 2013); or probing (Daumer, 220
 1958). Even finer gradations can be achieved—see Evan- 221
 gelista et al. (2010) for details on the moments before 222
 touchdown in honeybees. Some of these different behav- 223
 iours are sometimes lumped together and discussed as 224
 ‘preference’ even though floral choice consists of a series of 225
 sequential decisions that are not necessarily governed by the 226
 same parameters (Lunau, 1992; Lunau et al., 2006). 227

Individual differences 228

Individual differences in the behaviour of eusocial insects 229
 are pronounced and their origins are beginning to be 230
 understood (Jeanne, 1988; Jeanson and Weidenmüller, 231
 2013). For instance, task specialization is seen in honey- 232
 bees, and a colony even comprises both “employed” and 233
 “unemployed” foragers (Seeley, 1995). In bumblebees, 234
 there is some division of labour with smaller bees tending to 235
 the nest and larger bees devoting themselves more to for- 236
 aging (Goulson et al., 2002). Foraging effort is anything but 237



Fig. 2 *B. impatiens* worker tagged with RFID chip. © L.L. Orbán

238 evenly shared (Free, 1955). Individual differences are not
 239 especially problematic in procedures where the number of
 240 unrewarded choices of stimuli is fixed. When bees are given
 241 unrestricted access to a flight cage, however, some bees will
 242 invariably make considerably more choices than others, and
 243 the issue arises as to their representativeness. A sample of
 244 undifferentiated ‘bee-choices’ (e.g. Lehrer et al., 1995)
 245 gives little guide as to whether the results might reflect the
 246 behaviour of only a few particularly active bees. Individual
 247 differences (e.g. Orbán and Plowright, 2013), colony dif-
 248 ferences (Plowright et al., 2011) and population differences
 249 (Skorupski et al., 2007; Ings et al., 2009) have been
 250 reported.

251 Automation

252 Concerns over observer bias are common to many areas in
 253 the study of insect behaviour (Döring and Chittka, 2011), as
 254 are concerns over cost-effectiveness. The problems associ-
 255 ated with human monitoring of flower-naïve bee behaviour,
 256 in real time, are compounded here because the occurrence of
 257 rare events over long observation periods almost inevitably
 258 leads to decreases in vigilance (Warm et al., 2009).

259 Two low-cost technological advances are now available:
 260 (1) while video recordings are commonplace (Leonard and
 261 Papaj, 2011), motion-sensitive camcorders (Lihoreau et al.,
 262 2012; Orbán and Plowright, 2013) have the added advan-
 263 tage of recording a specified length clip only when a specific
 264 pattern of movement is detected in the viewfinder. This
 265 feature is particularly well suited to our situation because it
 266 filters out much of the time during which there is no activity
 267 around the stimuli. (2) Radio-frequency identification

(RFID) is analogous to the bar-coding system that was
 268 pioneered by Buchmann for the identification of honeybees
 269 (the unpublished method is described by Reynolds and
 270 Riley (2002)). A metallic identification tag is glued to the
 271 thorax (see Fig. 2) and detected by a reader placed at stra-
 272 tegic locations (Streit et al., 2003; Sumner et al., 2007;
 273 Ohashi et al., 2010; Stelzer and Chittka, 2010; Decourtye
 274 et al., 2011; Silcox et al., 2011; Nachev et al., 2012; Kat-
 275 zenberger et al., 2013). We have recently adapted the
 276 technology to detect flower-naïve bumblebees exploring
 277 unrewarding flowers (Orbán and Plowright, 2013). A video
 278 illustration of the procedure is shown by Orbán and Plo-
 279 wright (2014). One limitation of the method is the detection
 280 distance being restricted to a few millimetres (for other
 281 design considerations; see Carbutar et al. 2009). Electro-
 282 magnetic sensors to detect approach of flowers (Heuschen
 283 et al., 2005), used in conjunction with RFID, would be
 284 helpful in tracking behavioural sequences. 285

286 Preferences of flower-naïve honeybees and bumblebees

287 A casual observer who has ever seen a bee land on the floral
 288 picture on a seed packet or the floral print on an article of
 289 clothing may have had the distinct impression that the bee
 290 had been fooled: in the absence of discrimination training
 291 between flowers and pictures of flowers (Thompson and
 292 Plowright, 2014), the bees seem to have confused the two. A
 293 compelling demonstration is provided by Chittka and
 294 Walker (2006): bumblebees (*Bombus terrestris*) spontane-
 295 ously land preferentially on Van Gogh’s *Sunflowers* rather
 296 than Caulfield’s *Pottery*. In our lab, we have seen a flower-
 297 naïve bumblebee probe a photograph of a flower (see
 298 Fig. 3). Here, we consider what might be floral features that
 299 are particularly alluring.

300 Colour

301 Colour perception

302 Unlearned colour preference is the most intensively studied
 303 floral visual property that includes the investigation of dif-
 304 ferent frequencies of the electromagnetic spectrum, colour
 305 saturation, and contrast between patterns and backgrounds.
 306 Neurophysiological experiments show that bumblebees and
 307 honeybees have peak spectral sensitivities at approximately
 308 350, 450 and 550 nm, which correspond to ultra-violet
 309 (UV), blue and green regions of the spectrum (Peitsch et al.,
 310 1992; Skorupski et al., 2007). There are no receptors with
 311 peak sensitivity near red, which likely accounts for poor
 312 learning of red (Chittka, 1997; Lunau et al., 2011), even in
 313 species (e.g. *Bombus dahlbomii* Guérin-Méneville, 1835)
 314 that are known to visit red flowers (Martínez-Harms et al.,



Fig. 3 Flower-naïve bumblebee (*B. impatiens*) extending its proboscis towards a photograph of a flower. © V. Simonds. Photograph reproduced with permission

2010). Colour vision functions only, however, at relatively short distances: up to 10 cm for a grating with a spatial period of 2 cm, or subtending an angle of 15° in honeybees, but only 2.7° in bumblebees (Lehrer et al., 1988; Land, 1997; Macuda et al., 2001; Chittka and Raine, 2006). Honeybees use green-contrast (i.e., grayscale vision) to an angle subtending up to 5° (2.3° for bumblebees) but beyond this point, the shapes of objects become indistinguishable (Dyer et al., 2008). The evolution of insect colour vision is reviewed by Briscoe and Chittka (2001).

The fact that bees have sensitivity in the UV range of the spectrum is particularly important for plant–pollinator interactions. Ultraviolet absorbing “floral guides” that are invisible to humans are perceptible to pollinators. Not only do they serve to orient bees at close range towards the source of reward, but they also affect visitation rates (Horth et al., 2014). The appearance of flowers revealed by UV photography is illustrated in Fig. 4. In a manipulation of UV properties, Koski and Ashman (2014) have demonstrated that it is not the UV reflectance or absorbance alone but the patterns created on flowers that are attractive to pollinators.

The colour of nectar guides was studied on four spectral frequencies of 41 flower species: wavelengths of 360 nm (ultraviolet), 450 nm (blue), 520 nm (green) and 680 nm (red) (Penny, 1983). Flowers displayed nectar guides with better colour contrast on the insect visible spectrum (360 and 450 nm) when compared with the human visible spectrum (520 and 680 nm). The colour contrast effect was weaker when only UV was considered, suggesting that UV does not have a disproportionate contribution to preference: bees will choose yellow, and violet as well as UV. This behavioural finding about bee’s preference for several distinct colours is consistent with a study that showed non-UV flower colours are more common than UV flowers (Chittka et al., 1994), and another study that highlights the absence of pure UV flowers (Menzel and Shmida, 1993). Indeed, there is general agreement that the salience of floral UV patterns

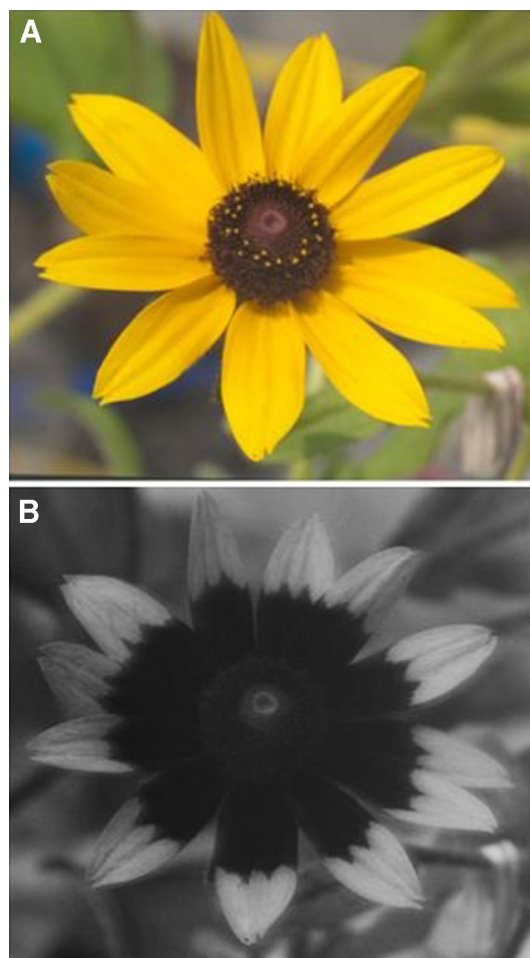


Fig. 4 *Rudbeckia hirta* as seen with colour photography. **b** *R. hirta* as seen with ultraviolet (UV) photography. Photograph reproduced from an Open Access article (Horth et al., 2014) under a Creative Commons Attribution Licence

is comparable to the salience of other colours visible to bees (Kevan et al., 2001).

Floral colours 354

The colour preferences of both honeybees and bumblebees prior to any experience with flowers have been reviewed by Lunau and Maier (1995). While bumblebees and honeybees have similar colour vision (Peitsch et al., 1992), they differ in that honeybees have a highly developed communication system: experienced honeybees communicate the location of food sources to inexperienced bees (von Frisch, 1967). Nonetheless, honeybees (*A. mellifera*) with controlled prior experience (“neutral pre-training”) do have colour preferences (Giurfa et al., 1995) for wavelengths of 410 nm (“bee-uv-blue”) and 530 nm (“bee-green”): the same colours that are learned most easily (Menzel, 1967). Bumblebees have, at most, a primitive communication system (Dornhaus and Chittka,

369 1999, 2001) and individuals rely much more on their own
370 efforts to find food.

371 The key dimension in triggering approach by untrained
372 bumblebees and honeybees is not so much the dominant
373 wavelength (giving rise to the perception of hue) of the
374 corolla of a flower, but its spectral purity (giving rise to the
375 perception of saturation), i.e. the degree to which there is
376 one dominant vs. a mix of wavelengths (Lunau, 1990, 1992;
377 Papiorek et al., 2013; Rohde et al., 2013). Corollas with high
378 spectral purity are approached from afar (Lunau et al.,
379 1996). Flowers incite inspection (*Bombus lucorum* (L.,
380 1761) and *B. terrestris* (L., 1758)) with a gradient of spectral
381 purity: low in the background, high at the corolla and
382 highest at floral guides such as stamens. Spectral purity acts
383 as a releaser for action patterns such as antennal reactions
384 (Lunau, 1991) and other optical signals of stamens, such as
385 size of the thecae and distance between them, elicit final
386 landing (Lunau, 1991). Most flowers are not single-col-
387 oured, and indeed two-coloured flowers are preferred
388 (Heuschen et al., 2005).

389 Floral size

390 Under the principle that the evolution of floral signals is tied
391 to pollinator perception, and that in nature floral size is
392 possibly predictive of reward, Blarer et al. (2002) consid-
393 ered the possibility that there might be a preference for large
394 flowers over smaller ones on the very first visit by bum-
395 blebees (*B. terrestris*). If such a preference were found, it
396 would be important in terms of the evolution of floral dis-
397 plays: plants that honestly signalled their reward availability
398 (see Armbruster et al., 2005) would be invisible by cheaters.
399 Such a preference was not found, though with experience,
400 bees were capable of associating floral size with reward
401 (Blarer et al., 2002). In a more recent study, we used arti-
402 ficial flowers that consisted of two blue perpendicular
403 acrylic sheets perched on top of a container that trapped
404 bees that entered. The design of these flowers was based on
405 traps used in the field to census insect populations (Stephen
406 and Rao, 2005). We manipulated the size of the flowers, but
407 no effect on the choices of flower-naïve bumblebees (*B.*
408 *impatiens*) was detected (Hudon and Plowright, 2011). The
409 usual cautions in interpreting failures to reject the null
410 hypothesis apply.

411 Patterning

412 Floral guides

413 The suggestion that floral markings function to guide poll-
414 inators towards the nectary likely originated with Sprengel
415 (1793). When patterns are presented at the ends of corridors
416 in a maze, selective approach of radial patterns (i.e.

‘sunburst’ patterns: alternating black and white pie shaped
segments, all pointing to the centre) over concentric patterns
(i.e. ‘bull’s eye’ patterns: alternating black and white circles
within each other) has been well documented for honeybees
(Lehrer et al., 1995) and bumblebees (Simonds and Plo-
wright, 2004; Plowright et al., 2006; Séguin and Plowright,
2008). Selective landing on radial patterns by free flying
bumblebees has also been reported (Orbán and Plowright,
2013). Whether flowers have petals or not seems compar-
atively unimportant: it is the presence of radial lines on
artificial flowers that causes bumblebees not only to make
their first landing but also to locate food more quickly after
landing (Leonard and Papaj, 2011). These lines are benefi-
cial for the plants: they discourage nectar robbing (Leonard
and Masek, 2014). Experimental removal of “floral sign-
posts” has a detrimental effect on plant fitness (Hansen
et al., 2012; Whitney et al., 2013).

While the evidence above shows that “X marks the spot”
(Leonard and Papaj, 2011), other shapes also seem to be
used as floral guides. Flowers with a dot or pair of dots at the
centre of flower (Fig. 1) are more likely to be approached
and antennated by flower-naïve bumblebees (Heuschen
et al., 2005), with bigger dots eliciting stronger responses by
both honeybees and bumblebees (Lunau et al., 2009).

Pattern location

The case for special markings functioning as guides to the
nectary or to the anthers is bolstered by a recent experiment
where the presence of the food source was dissociated from
the place indicated by the guide. When the position of the
nectary conflicted with the ‘directions’ given by an off-
centre guide, unsuccessful novice bumblebee foragers spent
significantly more time searching for nectar than when the
nectar guides surrounded the nectary (Goodale et al., 2014).
Using a similar experimental strategy of dissociating two
variables, pattern type (radial vs. concentric) and location of
the pattern elements (central vs. peripheral), we showed that
both concentric elements and radial elements caused bum-
blebees to enter an artificial flower, as long as the elements
were centrally located: both ‘X’ and ‘O’ marked the spot.
Concentric elements at the periphery of the flower put
bumblebees that had landed on the flower on a circular path
that steered them clear of the centre. Landing was more
likely on artificial flowers displaying radial elements,
regardless of whether they were positioned centrally or
peripherally (Orbán and Plowright, 2013).

Spatial frequency

In nature, some plants make themselves detectable not by
their particularly large floral structures, but by their inflo-
rescences consisting of clusters of small flowers (Lehrer

466 et al., 1995): spatial frequency (i.e. the “busyness”) of the
 467 visual input may be a key variable. Honeybees show a
 468 gradient of strong to weak preference for clusters consisting
 469 of four, three, two or one radiating patterns. In comparison
 470 of various spatial frequencies for each of several patterns
 471 (horizontal gratings, vertical gratings, radial patterns and
 472 concentric circles), however, a consistent preference for
 473 comparatively low frequencies was obtained, even though
 474 the most disrupted patterns were resolvable—i.e. the lines
 475 were not perceived as blurred together (Lehrer et al., 1995).
 476 Preferences for relatively high spatial frequency patterns
 477 have also been reported (Dafni et al., 1997; Plowright et al.,
 478 2011). Several possible explanations might account for the
 479 discrepancies across studies: (1) the absolute values for
 480 spatial frequencies likely differ across studies, with “high”
 481 and “low” being relative terms. (2) It is not so much the
 482 spatial frequency per se that is important, as it is the asso-
 483 ciated contrast with the background, as suggested by Lehrer
 484 et al. (1995)—indeed, even colour preferences of bumble-
 485 bees are affected by background complexity (Forrest and
 486 Thomson, 2009). (3) As suggested below, the effect of
 487 spatial frequency may depend on another variable:
 488 symmetry.

489 Symmetry

490 An important consideration with regard to what draws bees
 491 to flowers for the first time is how easy it is to encode and
 492 remember a floral pattern should it turn out to be rewarding.
 493 In other words, perceptibility, learnability and memorability
 494 of the pattern may turn out to be important aspects of what
 495 makes flowers attractive to bees. Indeed, Nachev (2014) has
 496 recently made the case for “cognition mediated evolution”.
 497 This consideration puts the study of floral preferences
 498 squarely in the domain of psychology. Cognition, percep-
 499 tion, neuroscience and computational modelling are here at
 500 centre stage.

501 The evolution of floral symmetry has been reviewed by
 502 Neal et al. (1998). Preferences for floral symmetry have
 503 been documented in the field. Naturally occurring sym-
 504 metric flowers of fireweed (*Epilobium angustifolium*) were
 505 preferentially visited by *B. terrestris*, and this was also true
 506 of experimentally manipulated flowers that affected sym-
 507 metry (Møller, 1995; see also Møller and Sorci, 1998). In
 508 the lab, honeybees perceive symmetry, as evidenced by
 509 their ability to learn discriminations between symmetric and
 510 asymmetric patterns and to generalize this learning to novel
 511 patterns (Giurfa et al., 1996). The evidence on a preference
 512 for symmetry by flower-naïve bees, however, is mixed. No
 513 such preference was reported by West and Laverty (1998),
 514 though bumblebees could learn that symmetric flowers were
 515 rewarding just as easily as they could learn that asymmetric
 516 flowers were rewarding. An “innate” preference for

517 symmetry about the vertical axis (i.e. bilateral symmetry) on
 518 vertically presented flowers (so the line of approach was
 519 perpendicular to the plane on which the pattern was pre-
 520 sented) by bumblebees was reported by Rodríguez et al.
 521 (2004). It seems, however, to have been the product of pre-
 522 training on rewarding discs (Plowright et al., 2011): truly
 523 flower-naïve bumblebees showed no preference for bilateral
 524 symmetry in vertically presented flowers. More recently,
 525 however, a preference for symmetry was found by
 526 increasing the strength of the manipulation: patterns for
 527 which there were four axes of symmetry, and not just one,
 528 were indeed chosen over asymmetric patterns (Orbán,
 529 2014).

530 Symmetry in flowers may well be an index of floral
 531 reward (Møller and Eriksson, 1995). Symmetry also affords
 532 considerable savings in terms of information processing
 533 since part of the pattern (half or even more, depending on
 534 the number of axes of symmetry) can be discarded without
 535 losing any information to be remembered. The cost of
 536 information processing may well translate into metabolic
 537 costs (Laughlin et al., 1998) and bees may act to minimize
 538 these costs as they search for flowers. A key point is that
 539 symmetry simplifies the processing of a complex pattern,
 540 and low spatial frequency simplifies the processing of an
 541 asymmetric pattern: the effect of one variable should
 542 depend on another. This notion of computational savings
 543 was captured in a mathematical model of pattern recon-
 544 struction (ICA: Independent Component Analysis; Orbán
 545 and Chartier, 2013). The essence of ICA is that the visual
 546 system completes a process akin to a dimensionality
 547 reduction process whereby the raw visual input is reduced to
 548 a small set of descriptive features. The model made novel
 549 predictions that were borne out empirically. For instance, a
 550 preference for low spatial frequency patterns over high-
 551 frequency patterns was found, but this preference was only
 552 detected when the patterns were ‘cumbersome’ by virtue of
 553 being asymmetric.

Social cues

554 Up to now we have been considering aspects of flowers that
 555 elicit initial choice. Recent research has addressed the
 556 question of whether the presence of foragers on flowers
 557 functions the same way as floral properties: perhaps an
 558 individual on a flower attracts other bees towards it. From a
 559 mechanistic point of view, local enhancement or stimulus
 560 enhancement, whereby one individual attracts another to a
 561 particular location or stimulus, is commonplace in animal
 562 behaviour (Shettleworth, 2010). From a functional point of
 563 view, however, such a possibility is only one of other
 564 plausible scenarios. Perhaps in nature floral characteristics
 565 are such strong predictors of reward that additional social
 566 cues carry little additional informational value. Another
 567

possibility is that while the presence of a forager signals that a flower has indeed been discovered, it also signals that the flower is empty or on its way to being depleted. In other words, other foragers may act as informers or as competitors (Baude et al., 2011). In view of these considerations, it might be expected that the predictive value of the presence of other foragers on flowers might depend on local environmental conditions and might only be learned from experience. We turn now to the evidence on this point.

Recent reports have shown that a preference for “occupied” flowers is not only modified by rewarded experience (Leadbeater and Chittka, 2009; Avarguès-Weber and Chittka, 2014), but is also apparent as soon as bees first begin to search for food. Inexperienced bumblebees given a choice between two rewarding artificial flowers, one of which was occupied by a dead pinned bee and the other not, first landed on the occupied flower more frequently than chance (Kawaguchi et al., 2006). Similarly, inexperienced bumblebees given a choice amongst 12 unrewarding artificial flowers, four of which were occupied by a dead pinned bee and eight of which were not, first landed on an occupied flower more frequently than chance (Leadbeater and Chittka, 2009). A preference for occupied stimuli was also found by Plowright et al. (2013), but only under a restricted set of conditions: when the occupied flowers were comparatively rare, and in addition, the ratio of the size of the occupier relative to the size of the flower was comparatively large. Otherwise, choice proportions did not differ from chance.

Little is known about how the presence of other foragers is perceived by bees making floral choices. They may be possibly perceived as being parts of the flowers such as nectar guides (Baude et al., 2008), or they may be perceived as other inanimate objects such as a coin or a plastic disc (Dawson and Chittka, 2012). There is evidence that flowers have adapted their visual appearance to exploit the salience provided by the presence of other foragers. For example, a South-African daisy species (*Gorteria diffusa*) displays insect-mimicking petal spots (Thomas et al., 2009; Whitney et al., 2011).

607 Conclusion

608 Bees discover all kinds of flowers that have few similarities.
609 Lilacs (*Syringa vulgaris*), comfrey (*Symphytum officinale*),
610 monkshood (*Aconitum* spp.), thistles (*Cirsium* spp.), blue-
611 berry and cranberry flowers (*Vaccinium* spp.), sunflowers
612 (*Helianthus annuus*) and tomato flowers (*Solanum lycopersicum*)
613 do not share all the same colour, contrast, symmetry,
614 spatial frequency or size properties. Moreover, these flowers
615 do share at least some features with other objects that are not
616 flowers (e.g., leaves are usually symmetric; some insects

reflect UV). This review has shown that several floral properties are attractive to honeybees and bumblebees with no previous foraging experience, but there seems to be no single set of essential features that define the category of “food source” or even “possibly a food source”.

There is no shortage of problems and unanswered questions to address, of which we enumerate a few here for consideration in future research:

1. The question of the nature of experience, i.e. how the bee sees the world, remains open. Cautions against anthropomorphism abound, but they bear repeating. Not only do flowers that look the same to humans look different to bees by virtue of their UV patterns, but the reverse is also true: Dyer et al. (2007) have shown that two variants of snapdragon (*Antirrhinum majus*) look very different to humans but are treated as the same by bumblebees.
2. The question of how to bridge the gap between the lab studies delineated here and behaviour in the considerably larger scale environment in the field is also worthy of investigation for bees as it is for other animals (Shettleworth, 1989).
3. There are about 250 *Bombus* species worldwide (Williams and Osborne, 2009) and yet the research reviewed above has focused on a handful of easily available species such as *B. impatiens* and *B. terrestris*. There are fewer than ten *Apis* species, but one of them, *Apis mellifera*, has been over-represented in the research. Flower visitors specialize on certain plant traits (Junker et al., 2013) and generalizations based on a few species are almost certainly limited.
4. Our list of important visual cues, used in isolation or in conjunction with other cues, will likely expand with future research. Just recently, the use of polarization patterns by *B. terrestris* has been demonstrated in learned discriminations between artificial flowers (Foster et al., 2014). In the past, polarization had only been known to be important in navigation (Rossel, 1993).
5. The testing for the effect of variables one by one for their value as releasers is inefficient. A more contemporary approach would be to determine how bees classify multi-dimensional signals (Shettleworth, 2010). For instance, floral “salience”, which is a function of the intensity of several floral stimuli, turns out to be a parsimonious explanatory variable (Katzenberger et al., 2013).
6. Our purpose here was most certainly not to dissect behaviour into categories. It was to put the focus on the precursors of behaviour learned from experience with flowers: the scaffolding on which learning is built. These behaviours are likely to be important from a conservation point of view: though possible disruptions

669 in how bees first find food may turn out to be
670 inconsequential, it seems an unlikely scenario. Ulti-
671 mately, however, the goal is to understand the
672 development of functional behaviour. Future research
673 should be aimed at linking what we know about the
674 behaviours of comparatively inexperienced workers
675 with what we know about experienced workers. Several
676 recent studies have investigated the fate of the prefer-
677 ences that guide bees to their first floral contact: How
678 easily are they forgotten (Milet-Pinheiro et al., 2012)?
679 Are they distracting (Morawetz et al., 2013)? Can they
680 be associated with consequences such as rewards or
681 punishers (Pohl et al., 2008)? Given the current
682 research effort aimed at protecting pollinators in
683 general, at protecting bees in particular, and especially
684 at understanding ‘the plight of the bumblebee’, none of
685 these questions are idle.

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