

1 **Treating hummingbirds as feathered bees: a case of ethological cross-pollination**

2 Pritchard, D.J., Tello Ramos, M.C., Muth, F., & Healy, S.D.

3 Running title: foraging cognition in hummingbirds and bees

4

5

6

7

8

9

10

11 Published in *Biology Letters*, 2017, 13 (12) by The Royal Society. The final published version is available  
12 at <https://doi.org/10.1098/rsbl.2017.0610>

13

14

15

16

17

18

19

20

21

22 **Abstract**

23 Hummingbirds feed from hundreds of flowers every day. The properties of these flowers provide  
24 these birds with a wealth of information about colour, space, and time to guide how they forage. To  
25 understand how hummingbirds might use this information, researchers have adapted established  
26 laboratory paradigms for use in the field. In recent years, however, experimental inspiration has come  
27 less from other birds, and more from looking at other nectar-feeders, particularly honeybees and  
28 bumblebees, which have been models for foraging behaviour and cognition for over a century. In a  
29 world in which the cognitive abilities of bees regularly make the news, research on the influence of  
30 ecology and sensory systems on bee behaviour is leading to novel insights in hummingbird cognition.  
31 As methods designed to study insects in the lab are being applied to hummingbirds in the field,  
32 converging methods can help us identify and understand convergence in cognition, behaviour and  
33 ecology.

34

35

36

37

38

39

40

41

42

43 **Introduction**

44 Birds and bees have a history of being lumped together. In medieval times, bees were considered “the  
45 smallest of birds” [1], whereas today the smallest known species of bird, weighing less than 2g, is

46 called the “bee hummingbird” *Mellisuga helenae*. But their small size, buzzing flight, and visits to  
47 flowers, have led many species of hummingbird to be coupled with bees in the popular imagination. It  
48 is no coincidence, for example, that both the Japanese (ハチドリ) and Chinese (蜂鸟) words for  
49 “hummingbird” literally translate as “bee bird”. In the natural world too, hummingbirds may share the  
50 same fields of flowers with the eusocial bees, particularly bumblebees *Bombus* and honeybees *Apis*, if  
51 not necessarily the same flowers.

52         Although often compared in their capacity as pollinators, hummingbirds and bees have long  
53 been studied by observers curious about their foraging decisions. The need to visit so many flowers  
54 every day, as well as the sensory signals offered by the brightly coloured flowers they visit, cannot  
55 help but provoke questions about what hummingbirds and bees might learn while foraging. On  
56 occasion, their shared ecology has led to hummingbirds and bees being directly compared to one  
57 another, or methods used with bees, applied to studying hummingbirds. Over time, however, the  
58 research studying these different nectar-feeders had grown apart. Field studies of hummingbird  
59 cognition were not designed with reference to bees, but instead to food-storing birds and to examine  
60 the role of cognitive representations such as local and global spatial memory. In contrast, free-flying  
61 bees were used to examine the cognitive mechanisms underlying foraging decisions, how bees  
62 navigate to familiar flowers, and how their foraging behaviour adapts to different distributions of  
63 resources.

64         Studying abstract cognitive abilities in bees, however, is now in vogue, while methods and  
65 ideas derived from studies of bee navigation and behavioural ecology are changing the way we think  
66 about hummingbird cognition. In this review, we will move from a historical context, covering the  
67 last time that hummingbirds and bees were studied side-by-side, to developments that have paved the  
68 way for the current state of hummingbird cognition.

69

## 70 **Early Experiments**

71 The American ornithologist Frank Bené conducted early tests on colour preference of hummingbirds  
72 in his garden [e.g. 2]. Bené showed that hummingbirds learned about colours, rather than innately  
73 favouring red as previously believed [3], and described the key role that location plays in  
74 hummingbird memory. In the following passage he describes the effect of moving a feeder visited a  
75 few times by a female black-chin hummingbird 2 feet (60cm) horizontally and 10in (25.5cm)  
76 vertically:

77 *“When the bird arrived, she flew straight to the old site as though the vial was still there, but finding*  
78 *no feeder, became bewildered and excited. She searched for the vial, but either it escaped her*  
79 *attention or she failed to associate [the vial in the new location] with the original ... A few seconds*  
80 *later she left.”* (Bené, 1945: pg. 13).

81 Over the next 30 years, a number of studies followed a similar path, with most focussed on colour  
82 preference [e.g. 4,5]. With the 1970s, however, came behavioural ecology and with it optimal  
83 foraging theory. Foraging took centre-stage in the animal behaviour world, with models suggesting  
84 rules by which animals could maximise their net intake of energy [6]. As hummingbirds feed largely  
85 on sugar, the energetic costs and benefits of foraging were relatively straightforward to calculate [7],  
86 and the factors that made hummingbirds amenable to simple field experiments, e.g. ease of  
87 observation and discrete foraging decisions, meant that hummingbirds became prime candidates for  
88 testing these new theories.

89

## 90 **Optimal foraging in birds and bees**

91 From early experiments and observations by the likes of Fabre and Romanes, to the Nobel prize  
92 winning work of von Frisch, there is a long history of studying the behaviour of bees. However, it was  
93 in tests of optimal foraging theory that bees were compared directly to hummingbirds for the first  
94 time.

95 These studies demonstrated that hummingbirds and bees did not forage randomly. Rather,  
96 they avoided revisiting flowers more than expected by chance [8,9] and moved differently depending

97 on flower quality. Both hummingbirds and bees travelled further following visits to poorer quality or  
98 depleted flowers [10,11], remaining in profitable patches and moving out of unprofitable patches.

99           The drawback to these studies was, ironically, the theory that inspired them. Comparisons of  
100 hummingbirds and bees were based on animals using optimal “movement rules” or “departure rules”.  
101 Behaviour was mainly examined as distances and directions between flower choices, rather than  
102 aspects such as time and location. Sequences of choices were analysed for patterns that could  
103 represent possible movement rules, which became increasingly complex. One rule, for example, was  
104 for a bumblebee to move to the closest unvisited flower unless the last movement was downward or  
105 was the first movement in a patch [12].

106           Among the many conditions in this rule, the need to avoid “just visited” flowers highlights  
107 one way in which spatial memory could be seen as compatible with these movement rules. Avoiding  
108 the “just visited” flower could, for example, involve bees and hummingbirds using their memory to  
109 keep track of the flowers they have already visited to avoid revisiting them. This possibility was not  
110 taken particularly seriously in the earlier optimal foraging studies of hummingbirds and bees in favour  
111 of constraints, presumably movement rules, which reduced the probability of revisits to near-zero.  
112 The direction an animal had arrived at a flower was the only memory suggested to influence foraging  
113 decisions, with larger memory “capacity” implying memory for more previous arrival directions.

114           The role that memory played reflects the paucity of influence of the relatively young field of  
115 animal cognition on more theoretically-minded early studies of optimal foraging, despite work on the  
116 learning abilities of hummingbirds and bees by Bené, von Frisch, and of memory systems by Menzel  
117 and colleagues [13]. For example, honeybees entrained their circadian cycle to the intervals at which  
118 they tended to forage, anticipating food as the relevant time approached [14] while bumblebees  
119 learned the rate at which the flower offered nectar [11], and the colour of rewarding flowers [15].  
120 Furthermore, bumblebees had to learn how to manipulate flowers to reach the nectar they contained  
121 [16] using trial and error. This trial and error was related to the apparent difficulty of handling the  
122 flower: at more morphologically complex flowers bees took longer and had to visit more flowers  
123 before realising success.

124           Whereas early evidence for learning in foraging bees involved bees learning flower colour,  
125 morphology, or reward, in hummingbirds the spatial location of flowers appeared of primary  
126 importance [17]. Hummingbirds learned to prioritise visits to artificially enriched patches of flowers  
127 [18] and would preferentially visit flowers on the edges of their territory in the morning and more  
128 central flowers in the afternoon [19]. Some hummingbirds also returned to flowers at discrete but  
129 locations distant from each other, at regular intervals [e.g. 20]. This behaviour suggested that some  
130 hummingbird species might form repeated routes, or “trap-lines” between flowers, a behaviour first  
131 described in euglossine bees [21], which requires learning the location, and possibly the refill interval,  
132 of multiple flowers.

133

#### 134 **Hummingbirds meet Animal Cognition**

135 Since the heyday of optimal foraging, much of the research on learning and memory in foraging in  
136 bees has fallen into three, somewhat overlapping, areas. First, Menzel and colleagues in the 1970s and  
137 80s brought a combination of behaviour and neuroscience to short and long-term memory in both  
138 free-flying and harnessed bees [13], leading to other aspects of cognition and perception in the 1990s  
139 and early 2000s, including categorisation, attention, and, later, behaviours described as displaying  
140 “complex” cognition [22,23]. Secondly, by analysing the behaviour of navigating bees and other  
141 insects in detail, researchers such as Land, Collett and Cartwright described how insects learn a  
142 location in terms of a collection of remembered views [24]. This approach would later include  
143 bumblebees and other insects [e.g. 25], be applied to detailed analyses of specialised behaviours such  
144 as learning flights [e.g. 26], and employed to test the role that the visual flow of information across  
145 the retina (optic flow) plays in perceiving depth [27] and controlling flight [28]. Finally, the 1980s  
146 and 90s saw behavioural ecologists continue to probe at the ecological importance of bee foraging.  
147 Questions included the co-evolutionary relationship between bees and the flowers they pollinate,  
148 naturalistic foraging by bees over longer periods of time, and how experience shaped foraging  
149 behaviour in natural situations, including trap-lining. In the 21<sup>st</sup> century, the literature examining what

150 and how foraging bees learn about their flowers is both impressively diverse and intellectually  
151 vibrant.

152 Work on hummingbirds across this period were not so much inspired by bees but by other  
153 birds. During the 1980s and early 90s behavioural ecologists and comparative psychologists  
154 collaborated to understand the psychological mechanisms underlying natural behaviours, aiming to  
155 examine whether and how natural selection has shaped animal cognition [e.g. 29]. Although inspired  
156 by an animal's ecology, the methods used were typically taken from experimental psychology, rather  
157 than the naturalistic foraging tasks used in studies of bees. For example, in an analogue of the radial  
158 maze, hummingbirds kept track of "emptied" and "not-emptied" flowers [30]. Subsequent adaptations  
159 of laboratory paradigms included delayed-match-to-sample [31,32] and putting "local" and "global"  
160 cues in conflict [33]. Although rather vague on the information that hummingbirds actually used, e.g.  
161 "global cues", these psychologically-inspired studies demonstrated the learning capabilities of wild  
162 hummingbirds. These experimental methods showed that hummingbirds relied on spatial location  
163 over flower appearance [31,32], could learn a location after a single visit [32,34], distinguished  
164 between seen-but-unvisited flowers and novel flowers [35], learned spatial location faster with  
165 differently coloured flowers [36], and could learn the contents and refill rates of different flowers [37–  
166 39].

167 A drawback to this psychologically-inspired approach is that the "cues" it tested were defined  
168 only in very general terms, e.g. local v.s. global cues, rather in terms of the information hummingbirds  
169 in the wild were actually using. What, for example, is a "global" cue, to a hummingbird tested in a  
170 mountain valley? Flightpaths of the birds revealed that hummingbirds trained to visit a prominent, red  
171 artificial flower, and tested with the flower either moved 1.3-1.7 m or removed entirely, initially  
172 searched where the flower used to be. This suggested that hummingbirds do not relocate flowers by  
173 looking for them and flying in that direction, no matter how conspicuous the flowers [40]. What they  
174 actually did use to relocate a flower remained a mystery.

175

176 **Where are we now?**

177 From the early studies of optimal foraging to more recent investigations of learning and memory,  
178 there is now a large and diverse literature on foraging cognition in bees encompassing neurobiology,  
179 sensory ecology, and behavioural ecology. Studies of hummingbird foraging cognition over this  
180 period has tended to remain separate from these studies of bees, although this is now beginning to  
181 change. Bees are now providing inspiration for hummingbird researchers who are looking at their  
182 questions from a new perspective either by adopting methods more commonly used with insects or by  
183 testing insect-inspired hypotheses in hummingbirds. Two examples which demonstrate this “feathered  
184 bee” perspective follow.

185

186 **Case study 1: Trap-lining**

187 In addition to learning intervals between flower visits, hummingbirds can also use circadian timing  
188 and ordinal timing to keep track of flowers in different locations [e.g. 41]. The use of circadian timing  
189 is consistent with the time-of-day dependence of some hummingbird foraging [19], and with the well-  
190 documented role that circadian rhythms play in foraging in other animals. The use of ordinal timing  
191 was a bit more surprising, but was apparently crucial for successfully tracking which flowers were  
192 rewarded. In order to time their visits appropriately, hummingbirds learned both the time of day  
193 together with the order in which flowers were rewarded. When flowers were presented at the  
194 appropriate time of day but out of order, for example, by presenting the flowers for the first time in a  
195 day at the time at which the third patch had been rewarded, hummingbirds foraged randomly [41].

196       Animals in the laboratory can be trained to learn arbitrary sequences of choices or actions, but  
197 this training requires hundreds of sessions [e.g. 42]. Rufous hummingbirds, however, when foraging  
198 from a number of patches each of which contained reward only at a certain times of the day, learned  
199 the sequence of rewarded patches within a single day. This affinity for learning a sequence of rewards  
200 is akin to the trap-lining behaviour previously described for non-territorial hummingbirds. Although  
201 rufous hummingbirds are aggressively territorial and not traditionally considered as trap-liners, when

202 presented with multiple single flowers, they rapidly form one or two consistent routes between them  
203 [43].

204         This approach, in which hummingbirds were presented with increasing numbers of flowers  
205 rather than explicitly trained to a sequence, was inspired by work on trap-lining bees. Rather than  
206 training bees on prescribed sequences, researchers such as Thomson, Ohashi, Lihoreau, and Chittka,  
207 simply presented bees in the laboratory and in field arenas with artificial flowers that refilled after  
208 predetermined intervals [44,45]. Bumblebees spontaneously formed trap-lines between these locations  
209 and, similar to the hummingbirds [43], the route of their trap-line tended to follow the shortest  
210 possible route between the flowers. Nevertheless, the trap-lines of bees and hummingbirds do differ.  
211 For example, individual bees trap-line in either a clockwise or counter-clockwise direction around a  
212 patch of flowers, with most bees strongly preferring to fly in one of these two directions [45]. In  
213 contrast, individual hummingbirds, tested under the same conditions as traplining bees will switch  
214 between two or three trap-lines, with most showing no preference between flying clockwise or  
215 counter-clockwise [43]. Also, while both bumblebees and hummingbirds alter their trap-line in  
216 response to changes in the spatial geometry of the flowers, bumblebees will modify their route to  
217 prioritise highly rewarded locations [46], and hummingbirds modify their trap-lines only to avoid a  
218 poorly rewarded location. Both modifications of the foraging route, although slightly different,  
219 suggest that both bees and hummingbirds remember the location and quality of single flowers within  
220 their trap-lines, which is somewhat “episodic-like” in the combination of information on content,  
221 location, and time [47].

222         Despite differences in the duration of a bumblebee’s foraging life, which may be only a few  
223 weeks, and that of a hummingbird, which may live for multiple years, similarities in the formation and  
224 modification of trap-lines at smaller scales shows how hummingbirds and bees have converged in  
225 their responses to their foraging problems.

226

227 **Case study 2: View-based navigation**

228 How vertebrates remember spatial locations has been addressed predominantly from one of two  
229 perspectives: whether animals encode the overarching shape, or “geometry”, of their surroundings  
230 [48], such as the relative length of walls or the shape of an array of feeders, or, how animals use  
231 “landmarks”, which are usually discrete objects with a constant relationship to the goal [49]. Although  
232 early studies of how hummingbirds remembered space were heavily influenced by these laboratory  
233 studies of landmarks and geometry, hummingbirds did not use the “geometry” of an array of flowers  
234 or landmarks [50–52], except under very particular conditions [53]. Similarly, hummingbirds can use  
235 multiple landmarks to identify flower locations [50,52], but do so only under very particular  
236 conditions [54]. Overall, the approaches used by comparative cognition researchers to study spatial  
237 cognition in the laboratory have not proven to be particularly useful when studying hummingbirds in  
238 the field [55].

239         Rather than focussing on abstract qualities such as “landmarks” and “geometry”, research on  
240 spatial memory in bees has been directed at determining the sensory information available to  
241 navigating bees and how they use it to guide behaviour [56]. One of the insights of Cartwright and  
242 Collet [57], for example, was that a single view of a constellation of “landmarks” could provide  
243 spatial information. By matching the size and position of landmarks as projected on the retina, bees  
244 can pinpoint familiar locations without extracting abstract spatial cues such as “vectors” or  
245 “bearings”. Subsequent modelling and experiments on bees and other navigating insects has shown  
246 how information such as depth can be detected through patterns in optic flow [e.g. 27] and that even  
247 segmenting landmarks against the background might not be necessary for successful view-matching  
248 navigation [58]. View-based navigation now encompasses a wide range of strategies in which the  
249 visual information an animal perceives can itself lead an animal to its location, without the need for an  
250 animal to compute the spatial relationships between landmarks and a goal [59]. From experiments  
251 inspired by view-matching insects [e.g. 57], there is some evidence that hummingbirds might too  
252 relocate flowers using remembered views. When landmarks around a reward were made twice as  
253 large as in training, hummingbirds searched for the reward in locations that maintained the view, but  
254 not the distances, of the landmarks [work in review].

255           Recent developments in the capabilities of high-speed cameras and methods for tracking and  
256 reconstructing head movements are also allowing hummingbird researchers to look closer at the  
257 details of spatial behaviour. Detailed analyses of the head movements of navigating bees have shown  
258 how, rather than just learning a static snapshot, bees can use particular movements to extract and learn  
259 a rich and dynamic portrait of their surroundings. By moving their heads in ways that generate  
260 particular patterns of visual motion, bees and wasps can directly perceive the distances of different  
261 features [27], determine the distance of landmarks from a goal location [24], and shear 3D objects  
262 from their background [60]. Recently, these in-depth examinations of behaviour have been put  
263 together with cutting-edge view-reconstruction techniques, to gain a “view from the cockpit” of  
264 navigating wasps [61]. Although hummingbirds do not appear to show specialised learning  
265 behaviours, such as orientation flights, many birds show patterns of head movements associated with  
266 recognising objects and determining distances [62], behaviours that could affect what birds learn  
267 about spatial locations. The tools developed to study visual navigation in bees and other insects, could  
268 therefore allow hummingbird researchers to take a literal “bird’s eye view” of navigation, examining  
269 how views, behaviour, and landmarks come together to guide hummingbirds back to their flowers.

270

## 271 **Conclusion**

272           In recent years, eye-catching demonstrations of “complex” cognitive processes in bees have  
273 made headlines [e.g. 63, reviewed in 23]. Although removed from traditional studies of foraging bees,  
274 these studies have captured the attention of psychologists and biologists interested in the evolution of  
275 human cognition and raise the question of how tiny brains can produce such seemingly complex  
276 behaviour [22].

277           As studies of bee cognition appear to be increasingly influenced by the methods used to  
278 investigate, and questions asked of, vertebrate cognition, it is worth noting that this inspiration rarely  
279 goes in the other direction. Despite being discredited by evolutionary biology for over a century, the  
280 comparisons made in animal cognition still appear dominated by the “scala naturae”, assigning

281 species to a rung on a hypothetical evolutionary ladder. Although some species, such as corvids and  
282 cephalopods, may find themselves moving up the ladder following reports of their “sophisticated”  
283 cognition, most comparisons tend to look upwards. Thus, studies of fish or insects might look for  
284 cognitive abilities seen in birds and primates [e.g. 64], but it is rare for studies of birds and primates to  
285 look for abilities discovered in fish or insects. Research on hummingbird cognition represents an  
286 exception to this rule. Although separated by millions of years of evolution, and experiencing the  
287 world in vastly different ways, by ignoring the “scala naturae” in favour of ecology and treating  
288 hummingbirds as feathered bees, it is possible to look at birds that have been studied in one way or  
289 another for most of the twentieth century with fresh eyes. By focussing on the details of behaviour,  
290 the available visual information, and using naturalistic scenarios rather than elegant but contrived  
291 experimental designs, studies of bees are now inspiring a new generation of studies of hummingbirds.

292

## 293 **References**

- 294 1. In press. Medieval Bestiary : Bee. See <http://bestiary.ca/beasts/beast260.htm> (accessed on 22  
295 September 2017).
- 296 2. Bené F. 1945 The role of learning in the feeding behaviour of Black-Chinned Hummingbirds. *The*  
297 *Condor* **47**, 3–22.
- 298 3. Pickens AL. 1930 Favorite colors of hummingbirds. *The Auk* **47**, 346–352.  
299 (doi:10.2307/4075484)
- 300 4. Collias NE, Collias EC. 1968 Anna’s hummingbirds trained to select different colors in feeding.  
301 *The Condor* **70**, 273–274.
- 302 5. Lyerly SB, Riess BF, Ross S. 1950 Color preference in the Mexican Violet-eared hummingbird.  
303 *Behaviour* **2**, 237–248.
- 304 6. Stephens DW, Krebs JR. 1986 *Foraging Theory*. Princeton University Press.

- 305 7. Wolf LL, Hainsworth FR. 1971 Time and energy budgets of territorial hummingbirds. *Ecology*  
306 **52**, 980–988. (doi:10.2307/1933803)
- 307 8. Hainsworth FR, Mercier T, Wolf LL. 1983 Floral arrangements and hummingbird feeding.  
308 *Oecologia* **58**, 225–229.
- 309 9. Pyke GH. 1978 Optimal foraging: Movement patterns of bumblebees between inflorescences.  
310 *Theor. Popul. Biol.* **13**, 72–98. (doi:10.1016/0040-5809(78)90036-9)
- 311 10. Wolf LL, Hainsworth FR. 1990 Non-random foraging by hummingbirds: patterns of movement  
312 between *Ipomopsis aggregata* (Pursch) V. Grant inflorescences. *Funct. Ecol.* **4**, 149–157.  
313 (doi:10.2307/2389334)
- 314 11. Heinrich B. 1979 Resource heterogeneity and patterns of movement in foraging bumblebees.  
315 *Oecologia* **40**, 235–245.
- 316 12. Pyke GH. 1979 Optimal foraging in bumblebees: Rule of movement between flowers within  
317 inflorescences. *Anim. Behav.* **27**, 1167–1181. (doi:10.1016/0003-3472(79)90064-2)
- 318 13. Menzel R. 1999 Memory dynamics in the honeybee. *J. Comp. Physiol. A* **185**, 323–340.  
319 (doi:10.1007/s003590050392)
- 320 14. Frisch B, Aschoff J. 1987 Circadian rhythms in honeybees: entrainment by feeding cycles.  
321 *Physiol. Entomol.* **12**, 41–49. (doi:10.1111/j.1365-3032.1987.tb00722.x)
- 322 15. Heinrich B, Mudge PR, Deringis PG. 1977 Laboratory analysis of flower constancy in foraging  
323 bumblebees: *Bombus ternarius* and *B. terricola*. *Behav. Ecol. Sociobiol.* **2**, 247–265.  
324 (doi:10.1007/BF00299738)
- 325 16. Laverty TM. 1980 The flower-visiting behaviour of bumble bees: floral complexity and learning.  
326 *Can. J. Zool.* **58**, 1324–1335. (doi:10.1139/z80-184)

- 327 17. Cole S, Hainsworth FR, Kamil AC, Mercier T, Wolf LL. 1982 Spatial learning as an adaptation  
328 in hummingbirds. *Science* **217**, 655–7. (doi:10.1126/science.217.4560.655)
- 329 18. Gass CL, Sutherland GD. 1985 Specialization by territorial hummingbirds on experimentally  
330 enriched patches of flowers: energetic profitability and learning. *Can. J. Zool.* **63**, 2125–2133.  
331 (doi:10.1139/z85-313)
- 332 19. Paton D, Carpenter F. 1984 Peripheral foraging by territorial rufous hummingbirds: defense by  
333 exploitation. *Ecology* **65**, 1808–1819.
- 334 20. Gill FB. 1988 Trapline foraging by hermit hummingbirds: competition for an undefended,  
335 renewable resource. *Ecology* **69**, 1933–1942. (doi:10.2307/1941170)
- 336 21. Janzen DH. 1971 Euglossine bees as long-distance pollinators of tropical plants. *Science* **171**,  
337 203–205.
- 338 22. Giurfa M. 2007 Behavioral and neural analysis of associative learning in the honeybee: a taste  
339 from the magic well. *J. Comp. Physiol. A* **193**, 801–824. (doi:10.1007/s00359-007-0235-9)
- 340 23. Perry CJ, Barron AB, Chittka L. 2017 The frontiers of insect cognition. *Cobeha* **16**, 111–118.  
341 (doi:10.1016/j.cobeha.2017.05.011)
- 342 24. Collett M, Chittka L, Collett TS. 2013 Spatial memory in insect navigation. *Curr. Biol.* **23**, R789–  
343 R800. (doi:10.1016/j.cub.2013.07.020)
- 344 25. Riabinina O, de Ibarra NH, Philippides A., Collett TS. 2014 Head movements and the optic flow  
345 generated during the learning flights of bumblebees. *J. Exp. Biol.* **217**, 2633–2642.  
346 (doi:10.1242/jeb.102897)
- 347 26. Collett TS. 1995 Making learning easy: the acquisition of visual information during the  
348 orientation flights of social wasps. *J. Comp. Physiol. A* **177**. (doi:10.1007/BF00187632)

- 349 27. Lehrer M, Srinivasan MV, Zhang SW, Horridge GA. 1988 Motion cues provide the bee's visual  
350 world with a third dimension. *Nature* **332**, 356–357. (doi:10.1038/332356a0)
- 351 28. Srinivasan MV, Zhang SW, Lehrer M, Collett TS. 1996 Honeybee navigation en route to the  
352 goal: Visual flight control and odometry. *J. Exp. Biol.* **199**, 237–244.
- 353 29. Shettleworth SJ. 1993 Varieties of learning and memory in animals. *J. Exp. Psychol. Anim.*  
354 *Behav. Process.* **19**, 5–14. (doi:10.1037/0097-7403.19.1.5)
- 355 30. Healy SD, Hurly TA. 1995 Spatial memory in rufous hummingbirds (*Selasphorus rufus*): a field  
356 test. *Anim. Learn. Behav.* **23**, 63–68.
- 357 31. Tello-Ramos MC, Hurly TA, Healy SD. 2014 Female hummingbirds do not relocate rewards  
358 using colour cues. *Anim. Behav.* **93**, 129–133. (doi:10.1016/j.anbehav.2014.04.036)
- 359 32. Gonzalez-Gomez PL, Vasquez R a. 2006 A field study of spatial memory in green-backed  
360 firecrown hummingbirds (*Sephanoides sephaniodes*). *Ethology* **112**, 790–795.  
361 (doi:10.1111/j.1439-0310.2006.01223.x)
- 362 33. Healy SD, Hurly TA. 1998 Rufous Hummingbirds' (*Selasphorus rufus*) Memory for flowers:  
363 patterns or actual spatial locations? *J. Exp. Psychol. Anim. Behav. Process.* **24**, 396–404.
- 364 34. Flores-Abreu IN, Hurly TA, Healy SD. 2012 One-trial spatial learning: wild hummingbirds  
365 relocate a reward after a single visit. *Anim. Cogn.* **15**, 631–637. (doi:10.1007/s10071-012-0491-0)
- 366 35. Henderson J, Hurly TA, Healy SD. 2001 Rufous hummingbirds' memory for flower location.  
367 *Anim. Behav.* **61**, 981–986. (doi:10.1006/anbe.2000.1670)
- 368 36. Hurly TA, Healy SD. 2002 Cue learning by rufous hummingbirds (*Selasphorus rufus*). *J. Exp.*  
369 *Psychol. Anim. Behav. Process.* **28**, 209–223. (doi:10.1037//0097-7403.28.2.209)

- 370 37. González-Gómez PL, Bozinovic F, Vásquez RA. 2011 Elements of episodic-like memory in free-  
371 living hummingbirds, energetic consequences. *Anim. Behav.* **81**, 1257–1262.  
372 (doi:10.1016/j.anbehav.2011.03.014)
- 373 38. Henderson J, Hurly TA, Bateson M, Healy SD. 2006 Timing in free-living rufous hummingbirds,  
374 *Selasphorus rufus*. *Curr. Biol.* **16**, 512–515. (doi:10.1016/j.cub.2006.01.054)
- 375 39. González-Gómez PL, Vásquez RA., Bozinovic F. 2011 Flexibility of foraging behavior in  
376 hummingbirds: the role of energy constraints and cognitive abilities. *The Auk* **128**, 36–42.  
377 (doi:10.1525/auk.2011.10024)
- 378 40. Hurly TA, Franz S, Healy SD. 2010 Do rufous hummingbirds (*Selasphorus rufus*) use visual  
379 beacons? *Anim. Cogn.* **13**, 377–383. (doi:10.1007/s10071-009-0280-6)
- 380 41. Tello-Ramos MC, Hurly TA, Higgott C, Healy SD. 2015 Time–place learning in wild, free-living  
381 hummingbirds. *Anim. Behav.* **104**, 123–129. (doi:10.1016/j.anbehav.2015.03.015)
- 382 42. Orlov T, Amit DJ, Yakovlev V, Zohary E, Hochstein S. 2006 Memory of ordinal number  
383 categories in macaque monkeys. *J. Cogn. Neurosci.* **18**, 399–417.  
384 (doi:10.1162/jocn.2006.18.3.399)
- 385 43. Tello-Ramos MC, Hurly TA, Healy SD. 2015 Traplining in hummingbirds: flying short-distance  
386 sequences among several locations. *Behav. Ecol.* **26**, 812–819. (doi:10.1093/beheco/arv014)
- 387 44. Ohashi K, Thomson JD. 2009 Trapline foraging by pollinators: its ontogeny, economics and  
388 possible consequences for plants. *Ann. Bot.* **103**, 1365–1378. (doi:10.1093/aob/mcp088)
- 389 45. Lihoreau M, Chittka L, Raine NE, Kudo G. 2011 Trade-off between travel distance and  
390 prioritization of high-reward sites in traplining bumblebees. *Funct. Ecol.* **25**, 1284–1292.  
391 (doi:10.1111/j.1365-2435.2011.01881.x)

- 392 46. Lihoreau M, Chittka L, Raine NE. 2010 Travel optimization by foraging bumblebees through  
393 readjustments of traplines after discovery of new feeding locations. *Am. Nat.* **176**, 744–757.  
394 (doi:10.1086/657042)
- 395 47. Crystal, JD. 2010 Episodic-like memory in animals. *Behav. Brain Res.* **215**, 235–243.  
396 (doi:10.1016/j.bbr.2010.03.005)
- 397 48. Cheng K, Huttenlocher J, Newcombe NS. 2013 25 years of research on the use of geometry in  
398 spatial reorientation: a current theoretical perspective. *Psychon. Bull. Rev.* (doi:10.3758/s13423-  
399 013-0416-1)
- 400 49. Gould KL, Kelly DM, Kamil AC. 2010 What scatter-hoarding animals have taught us about  
401 small-scale navigation. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **365**, 901–914.  
402 (doi:10.1098/rstb.2009.0214)
- 403 50. Pritchard DJ, Scott RD, Healy SD, Hurly AT. 2016 Wild rufous hummingbirds use local  
404 landmarks to return to rewarded locations. *Behav. Processes* **122**.  
405 (doi:10.1016/j.beproc.2015.11.004)
- 406 51. Hornsby MAW, Hurly TA, Hamilton CE, Pritchard DJ, Healy SD. 2014 Wild, free-living rufous  
407 hummingbirds do not use geometric cues in a spatial task. *Behav. Processes* **108**, 138–41.  
408 (doi:10.1016/j.beproc.2014.10.003)
- 409 52. Hurly TA, Fox TAO, Zweste DM, Healy SD. 2014 Wild hummingbirds rely on landmarks not  
410 geometry when learning an array of flowers. *Anim. Cogn.* (doi:10.1007/s10071-014-0748-x)
- 411 53. Hornsby MAW, Healy SD, Hurly TA. 2017 Wild hummingbirds can use the geometry of a flower  
412 array. *Behav. Processes* **139**, 33–37. (doi:10.1016/j.beproc.2017.01.019)
- 413 54. Pritchard DJ, Hurly TA, Healy SD. 2015 Effects of landmark distance and stability on accuracy  
414 of reward relocation. *Anim. Cogn.* **18**. (doi:10.1007/s10071-015-0896-7)

- 415 55. Pritchard DJ, Hurly TA, Tello-Ramos MC, Healy SD. 2016 Why study cognition in the wild (and  
416 how to test it)? *J. Exp. Anal. Behav.* **105**. (doi:10.1002/jeab.195)
- 417 56. Zeil J. 2012 Visual homing: an insect perspective. *Curr. Opin. Neurobiol.* **22**, 285–293.  
418 (doi:10.1016/j.conb.2011.12.008)
- 419 57. Cartwright BA, Collett TS. 1983 Landmark learning in bees. *J. Comp. Physiol. A* **151**, 521–543.
- 420 58. Zeil J, Hofmann MI, Chahl JS. 2003 Catchment areas of panoramic snapshots in outdoor scenes.  
421 *J. Opt. Soc. Am. A* **20**, 450–69.
- 422 59. Wystrach A, Graham P. 2012 View-based matching can be more than image matching: The  
423 importance of considering an animal’s perspective. *i-Percept.* **3**, 547–9. (doi:10.1068/i0542ic)
- 424 60. Voss R, Zeil J. 1998 Active vision in insects: An analysis of object-directed zig-zag flights in  
425 wasps (*Odynerus spinipes*, Eumenidae). *J. Comp. Physiol. - Sens. Neural Behav. Physiol.* **182**,  
426 377–387. (doi:10.1007/s003590050187)
- 427 61. Stürzl W, Zeil J, Boeddeker N, Hemmi JM. 2016 How wasps acquire and use views for homing.  
428 *Curr. Biol.* **26**, 470–482. (doi:10.1016/j.cub.2015.12.052)
- 429 62. Kral K. 2003 Behavioural-analytical studies of the role of head movements in depth perception in  
430 insects, birds and mammals. *Behav. Processes* **64**, 1–12. (doi:10.1016/S0376-6357(03)00054-8)
- 431 63. Handwerk B. 2017 Bees Can Learn to Play “Soccer.” Score One for Insect Intelligence. *Smithson.*  
432 *Mag.* See [http://www.smithsonianmag.com/science-nature/bees-can-learn-play-soccer-score-one-](http://www.smithsonianmag.com/science-nature/bees-can-learn-play-soccer-score-one-insect-intelligence-180962292/)  
433 [insect-intelligence-180962292/](http://www.smithsonianmag.com/science-nature/bees-can-learn-play-soccer-score-one-insect-intelligence-180962292/) (accessed on 4 November 2017).
- 434 64. Bshary R, Wickler W, Fricke H. 2002 Fish cognition: a primate’s eye view. *Anim. Cogn.* **5**, 1–13.  
435 (doi:10.1007/s10071-001-0116-5)