

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

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3 Running title: foraging cognition in hummingbirds and bees

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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.

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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.

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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.

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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.

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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 21st 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.

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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.

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