

Review



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Animal behaviour

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

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

1. Introduction

Birds and bees have a history of being lumped together. In medieval times, bees were considered 'the smallest of birds' [1], whereas today the smallest known species of bird, weighing less than 2 g, is called the 'bee hummingbird' *Mellisuga helenae*. But their small size, buzzing flight and visits to flowers have led many species of hummingbird to be coupled with bees in the popular imagination. It is no coincidence, for example, that both the Japanese (ハチドリ) and Chinese (蜂鸟) words for 'hummingbird' literally translate as 'bee bird'. In the natural world too, hummingbirds may share the same fields of flowers with the eusocial bees, particularly bumblebees *Bombus* and honeybees *Apis*, if not necessarily the same flowers.

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

Studying abstract cognitive abilities in bees, however, is now in vogue, while methods and ideas derived from studies of bee navigation and behavioural ecology are changing the way we think about hummingbird cognition. In this review, we will move from a historical context, covering the last time that hummingbirds

and bees were studied side by side, to developments that have paved the way for the current state of hummingbird cognition.

2. Early experiments

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

When the bird arrived, she flew straight to the old site as though the vial was still there, but finding no feeder, became bewildered and excited. She searched for the vial, but either it escaped her attention or she failed to associate [the vial in the new location] with the original ... A few seconds later she left (Bené [2, p. 13]).

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

3. Optimal foraging in birds and bees

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

These studies demonstrated that hummingbirds and bees did not forage randomly. Rather, they avoided revisiting flowers more than expected by chance [8,9] and moved differently depending on flower quality. Both hummingbirds and bees travelled further following visits to poorer quality or depleted flowers [10,11], remaining in profitable patches and moving out of unprofitable patches.

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

Among the many conditions in this rule, the need to avoid 'just visited' flowers highlights one way in which spatial memory could be seen as compatible with these movement rules. Avoiding the 'just visited' flower could, for example, involve bees and hummingbirds using their memory to keep

track of the flowers they have already visited to avoid revisiting them. This possibility was not taken particularly seriously in the earlier optimal foraging studies of hummingbirds and bees in favour of constraints, presumably movement rules, that reduced the probability of revisits to near-zero. The direction from which an animal had arrived at a flower was the only memory suggested to influence foraging decisions, with larger memory 'capacity' implying memory for more previous arrival directions.

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

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

4. Hummingbirds meet animal cognition

Since the heyday of optimal foraging, much of the research on learning and memory in foraging bees has fallen into three, somewhat overlapping, areas. First, Menzel co-workers in the 1970s and 1980s brought a combination of behaviour and neuroscience to short- and long-term memory in both free-flying and harnessed bees [13], leading to other aspects of cognition and perception in the 1990s and early 2000s, including categorization, attention, and, later, behaviours described as displaying 'complex' cognition [22,23]. Second, by analysing the behaviour of navigating bees and other insects in detail, researchers such as Land, Collett and Cartwright described how insects learn a location in terms of a collection of remembered views [24]. This approach would later include bumblebees and other insects (e.g. [25]), be applied to detailed analyses of specialized behaviours such as learning flights (e.g. [26]), and employed to test the role that the visual flow of information across the retina (optic flow) plays in perceiving depth [27] and controlling flight [28]. Finally, the 1980s and 1990s saw behavioural ecologists continue to probe at the ecological importance of bee foraging. Questions included the coevolutionary relationship between bees and the flowers they pollinate, naturalistic foraging by bees over longer periods of time, and how experience shaped foraging behaviour in natural situations, including trap-lining.

In the twenty-first century, the literature examining what and how foraging bees learn about their flowers is impressively diverse and intellectually vibrant.

Works on hummingbirds across this period were not so much inspired by bees but by other birds. During the 1980s and early 1990s, behavioural ecologists and comparative psychologists collaborated to understand the psychological mechanisms underlying natural behaviours, aiming to examine whether and how natural selection has shaped animal cognition (e.g. [29]). Although inspired by an animal's ecology, the methods used were typically taken from experimental psychology, rather than the naturalistic foraging tasks used in studies of bees. For example, in an analogue of the radial maze, hummingbirds kept track of 'emptied' and 'not-emptied' flowers [30]. Subsequent adaptations of laboratory paradigms included delayed-match-to-sample [31,32] and putting 'local' and 'global' cues in conflict [33]. Although rather vague on the information that hummingbirds actually used, e.g. 'global cues', these psychologically inspired studies demonstrated the learning capabilities of wild hummingbirds. These experimental methods showed that hummingbirds that relied on spatial location over flower appearance [31,32] could learn a location after a single visit [32,34], distinguished between seen-but-unvisited flowers and novel flowers [35], learned spatial location faster with differently coloured flowers [36] and could learn the contents and refill rates of different flowers [37–39].

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

5. Where are we now?

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

6. Case study 1: trap-lining

In addition to learning intervals between flower visits, hummingbirds can also use circadian timing and ordinal timing to keep track of flowers in different locations (e.g. [41]). The use of circadian timing is consistent with the time-of-day dependence of some hummingbird foraging [19] and with the well-

documented role that circadian rhythms play in foraging in other animals. The use of ordinal timing was a bit more surprising, but was apparently crucial for successfully tracking which flowers were rewarded. In order to time their visits appropriately, hummingbirds learned the time of day together with the order in which flowers were rewarded. When flowers were presented at the appropriate time of day but out of order, for example, by presenting the flowers for the first time in a day at the time at which the third patch had been rewarded, hummingbirds foraged randomly [41].

Animals in the laboratory can be trained to learn arbitrary sequences of choices or actions, but this training requires hundreds of sessions (e.g. [42]). Rufous hummingbirds (*Selasphorus rufus*), however, when foraging from a number of patches each of which contained reward only at a certain time of the day, learned the sequence of rewarded patches within a single day. This affinity for learning a sequence of rewards is akin to the trap-lining behaviour previously described for non-territorial hummingbirds. Although rufous hummingbirds are aggressively territorial and not traditionally considered as trap-liners, when presented with multiple single flowers, they rapidly form one or two consistent routes between them [43].

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

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

7. Case study 2: view-based navigation

How vertebrates remember spatial locations has been addressed predominantly from one of two perspectives: whether animals encode the overarching shape, or 'geometry', of their surroundings [48], such as the relative length of walls or

the shape of an array of feeders, or, how animals use ‘landmarks’, which are usually discrete objects with a constant relationship to the goal [49]. Although early studies of how hummingbirds remembered space were heavily influenced by these laboratory studies of landmarks and geometry, hummingbirds did not use the ‘geometry’ of an array of flowers or landmarks [50–52], except under very particular conditions [53]. Similarly, hummingbirds can use multiple landmarks to identify flower locations [50,52], but do so only under very particular conditions [54]. Overall, the approaches used by comparative cognition researchers to study spatial cognition in the laboratory have not proved to be particularly useful when studying hummingbirds in the field [55].

Rather than focussing on abstract qualities such as ‘landmarks’ and ‘geometry’, research on spatial memory in bees has been directed at determining the sensory information available to navigating bees and how they use it to guide behaviour [56]. One of the insights of Cartwright and Collet [57], for example, was that a single view of a constellation of ‘landmarks’ could provide spatial information. By matching the size and position of landmarks as projected on the retina, bees can pinpoint familiar locations without extracting abstract spatial cues such as ‘vectors’ or ‘bearings’. Subsequent modelling and experiments on bees and other navigating insects have shown how information such as depth can be detected through patterns in optic flow (e.g. [27]) and that even segmenting landmarks against the background might not be necessary for successful view-matching navigation [58]. View-based navigation now encompasses a wide range of strategies in which the visual information an animal perceives can itself lead an animal to its location, without the need for an animal to compute the spatial relationships between landmarks and a goal [59]. From experiments inspired by view-matching insects (e.g. [57]), there is some evidence that hummingbirds might too relocate flowers using remembered views. When landmarks around a reward were made twice as large as in training, hummingbirds searched for the reward in locations that maintained the view, but not the distances, of the landmarks [60].

Recent developments in the capabilities of high-speed cameras and methods for tracking and reconstructing head movements are also allowing hummingbird researchers to look closer at the details of spatial behaviour. Detailed analyses of the head movements of navigating bees have shown how, rather than just learning a static snapshot, bees can use particular movements to extract and learn a rich and dynamic portrait of their surroundings. By moving their heads in ways that generate particular patterns of visual motion, bees and wasps can directly perceive the distances of different features [27], determine the distance of landmarks from a goal location [24], and shear three-dimensional objects from their background [61]. Recently, these in-depth examinations of behaviour have

been put together with cutting-edge view-reconstruction techniques to gain a ‘view from the cockpit’ of navigating wasps [62]. Although hummingbirds do not appear to show specialized learning behaviours, such as orientation flights, many birds show patterns of head movements associated with recognizing objects and determining distances [63], behaviours that could affect what birds learn about spatial locations. The tools developed to study visual navigation in bees and other insects could therefore allow hummingbird researchers to take a literal ‘bird’s eye view’ of navigation, examining how views, behaviour and landmarks come together to guide hummingbirds back to their flowers.

8. Conclusion

In recent years, eye-catching demonstrations of ‘complex’ cognitive processes in bees have made headlines (e.g. [64], reviewed in [23]). Although rather different from traditional studies of foraging bees, these studies have captured the attention of psychologists and biologists interested in the evolution of human cognition and raise the question of how tiny brains can produce such seemingly complex behaviour [22].

As studies of bee cognition appear to be increasingly influenced by the methods used to investigate, and questions asked of, vertebrate cognition, it is worth noting that this inspiration rarely goes in the other direction. Despite being discredited by evolutionary biology for over a century, the comparisons made in animal cognition still appear dominated by the ‘scala naturae’, assigning species to a rung on a hypothetical evolutionary ladder. Although some species, such as corvids and cephalopods, may find themselves moving up the ladder following reports of their ‘sophisticated’ cognition, most comparisons tend to look upwards. Thus, studies of fish or insects might look for cognitive abilities seen in birds and primates (e.g. [65]), but it is rare for studies of birds and primates to look for abilities discovered in fish or insects. Research on hummingbird cognition represents an exception to this rule. Although separated by millions of years of evolution, and experiencing the world in vastly different ways, by ignoring the ‘scala naturae’ in favour of ecology and treating hummingbirds as feathered bees, it is possible to look at birds that have been studied in one way or another for most of the twentieth century with fresh eyes. By focussing on the details of behaviour, the available visual information and by using naturalistic scenarios rather than elegant but contrived experimental designs, studies of bees are now inspiring a new generation of studies of hummingbirds.

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