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# Space, the original frontier

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Over fifty years of work on animal cognition, enthusiasms for different topics can wax and wane. Interest in spatial cognition, once popular, has more recently waned. Some of this change, however, is only apparent, as research on spatial cognition continues to evolve and produce new scientific innovations. Indeed, recent technological developments has enabled us to now address questions raised from classic early studies. Here we review several key examples where past and present research approaches have intersected to provide new answers to old questions concerning spatial memory in food-storing birds and other laboratory animals, navigation in birds and insects, and spatial cognition in wild hummingbirds.

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One of the great success stories of cognitive ecology is that of the discovery of the association between storing multiple food items, the memory demand for retrieving that food, the neural substrate (hippocampus), and spatial cognition. Birds that store more seeds, have a bigger hippocampus, and do better in spatial memory tasks. Despite the lack of sophisticated technology, by correctly coupling the subject species with a suitable question about cognition plus experimental designs accessible to wild animals, forty years later, this research still forms the foundation for research on cognitive ecology. The experimental designs, themselves adapted to test spatial cognition, are still used in behavioural ecology and other

fields such as behavioural neuroscience and developmental psychology [1]. Our aim is to provide a reminder that such foundational work continues to inform the field of animal cognition and beyond, and point to the ways in which new technology is allowing us to tap into previously inaccessible questions raised by classic studies.

## Cognition of the wild

Although the original spatial cognition work was conducted in the field, it quickly became apparent that the key manipulations would be conducted far more readily in the laboratory. Fortunately, wild-caught food storers adapted well to the laboratory environment, both in terms of survival and welfare as well as their amenability to experimental procedures: a variety of species (tits, chickadees, nutcrackers, jays) were readily trained and tested on a range of spatial tasks. Although this work often relied on traditional experimental psychology methods, such as spatial delayed-non-matching-to-sample tasks presented on touchscreens [2], birds were often tested in whole rooms allowing birds to fly from location to location in a 'nearer-realistic' spatial scale to that experienced in the wild [3]. By such means, tests of cognition 'of' the wild were achieved.

But the logistics of testing different mechanisms of spatial cognition of a wide range of taxa, in nearer-realistic spatial scales meant that this research was, and is, restricted in terms of where it can be conducted and which species can be studied. The experiments typically depend heavily on the spatial capacity of research facilities and remain limited to a relatively small number of institutions, typically wealthy universities or zoos. The species that lend themselves to spatial cognition assessment are also typically constrained to small animals, such as songbirds such as tits, chickadees and zebra finches *Taeniopygia guttata* [4], killifish *Kryptolebias marmoratus* and guppies *Poecilia reticulata* [5,6], poison frogs *Dendrobates auratus* [7**], or invertebrates [8], although not always [9,10]. This narrowing of logistically feasible species is one of the reasons that spatial cognition testing did not maintain its prominent position in animal cognition. The emphasis on studying species with 'extreme' spatial cognition demands, as are conspicuous for food-caching birds, also limited the scope of plausible species. Nonetheless, these laboratory-based experiments have popularised straightforward and standardized memory tests developed for laboratory animals (e.g. finding food hidden in covered wells) which have taken root in behavioural and cognitive ecology, planted the seeds for research on the genetic

basis of spatial cognition [11] as well as continuing to offer insights into the nature of adaptive specialisations [12]. Meanwhile, with the aid of cutting-edge technology, limitations of scope in laboratory-based studies has led to work on spatial cognition in the wild, specifically avian and insect navigation.

## Cognition in the wild

### Avian navigation

Most of what we know about the role of cognition in avian navigation comes from flights of homing pigeons (*Columba livia*). In the early days, these data were of homing speed or vanishing direction based on manipulations at the release site [13], but it is increasingly possible to examine the cognitive basis of vast-scale navigational feats in the wild due to the development of new technologies such as GPS, head tracking, and satellite tracking. These methods have enabled us to learn even more about homing pigeons, even though we already knew so much, such as how individual pigeons develop a unique route following visual landmarks [14], and how different cues are combined or compete [15], including landmarks and the sun compass [16] and visual and olfactory cues [17]. Now we can even get inside the head of a pigeon as it homes because hippocampal-lesioned birds are no longer lost once they disappear from view but can be tracked as they lose their way [18••,19].

By allowing for experiments at even larger scales, and in more challenging terrains, these technologies are transforming our understanding of spatial cognition in the wild, of real animals at ecological meaningful scales. Seabirds, like shearwaters and frigatebirds, can now be tracked as they travel over vast stretches of ocean without apparent landmarks and we are beginning to understand how they can reliably find their way home following long foraging trips at sea. Not that these data have necessarily overturned older data gained from homing pigeons as, like homing pigeons, these seabirds find their way home using both smell and sun compass to identify the necessary direction to travel home [20,21], although unlike pigeons, they do not appear to encode a route of visual features such as islands, failing to avoid islands in their path [22].

For over 50 years we have known that adult birds learn cues that allow them to compensate for displacement during migration in a way that first-time migrators (relying on an inherited migration programme) apparently could not [23]. But it is becoming clear that this familiar fact may not be a complete description. For example, in species with considerable variation in migratory routes, such as honey buzzards *Pernis ptilorhynchus*, learning may play a role in the migratory route birds develop [24]. In addition, using GPS-trackers, it is possible to identify when young birds (e.g. fledgling great frigatebirds *Fregata minor*) learn to compensate for wind displacement [25••],

while satellite-tracking shows that, after experimental displacements, young cuckoos *Cuculus canoris* can also return to an appropriate migratory route, just as do experienced adults [26].

### Insect navigation

Another of the great success stories in spatial cognition comes not from studying vast migratory journeys or even well-worn laboratory paradigms, but from pulling apart the sensory and cognitive basis of insect navigation. We include it here not least because this work, although addressed to questions familiar to those working on spatial cognition in vertebrates, rarely informs this latter research, which is disappointing and perhaps detrimental.

In recent years, significant advances have been made in the neural mechanisms controlling insect navigation [27], advances built on decades of field experiments [28]. As far back as the 1970s, field experiments with species such as the desert ant *Cataglyphis bicolor*, unravelled the key components of insect navigation: polarisation compass, panoramic visual memories, visual and physical odometry, and path integration [29]. This sturdy foundation of sensory cue use has allowed analysis of the ways insects combine different kinds of information [30] and how the memories for navigational information are acquired and used [31••].

Traditionally field experiments on insect navigation are relatively 'low-tech', with animals tested with simple artificial landmarks and tracked using pen and paper or, when close to the nest, filmed from above. In recent years this has changed with analysis of body position and orientation by hand or from video giving way to automatic image-based and radar tracking [32]. Estimates of the visual information insects experience have evolved from visual angles based on head position, to systematic analysis of panoramic images, to rendering 3D modelling of the environment [33]. By combining these tools with traditional behavioural experiments and observations, researchers have mapped the spatial memory of wild ants [34], unravelled how stereotyped 'learning flights' assist place learning in wild wasps [35], and captured how bumblebees' spatial behaviour develops over an individual's lifetime [36]. Alongside models analysing how the kinds of information insects experience in the wild could be used for robust and versatile navigation [37], these experiments have provided the framework for investigating the neural basis of insect navigation. Despite the obvious differences in their sensory and neural apparatus, suggestions that navigation by insects and vertebrates might share similar features [38] also offers opportunities for those studying spatial cognition and navigation in vertebrates not least for those vertebrate species sharing foraging problems with insects.

## Spatial cognition in wild hummingbirds

While technological advances, such as harmonic radar [32,39] and reflective tags [40] have allowed for the tracking of increasingly smaller animals like honeybees and bumblebees, there are some animals for which similar technological advances are still more a hope than a reality. One of these is the rufous hummingbird *Rufus selasphorus*, a species used to examine spatial cognition in the wild for almost three decades. These birds weigh around 3 g, heavy enough to bear the weight of a harmonic radar aerial but as they fly through open meadows and moderately dense woodland, their environment precludes such methodology. While waiting, we have managed to exploit the ease with which these wild hummingbirds can be trained to feed from artificial feeders to explore spatial cognition in the wild [41]. For over 70 years it has been clear that foraging for hummingbirds is a spatial memory task: field experiments consistently demonstrate that, given a choice between a flower of the same colour as that of a previously rewarded flower or a flower at the same spatial location, both territorial males and nonterritorial females revisit the flower at the correct spatial location [42,43].

Field experiments using modifications of laboratory experimental designs can add depth to our understanding of spatial cognition. For example, some of the first data on spatial performance in 3D showed that rats *Rattus norvegicus* and hummingbirds solve spatial problems differently, perhaps due to differences in their foraging ecology: while laboratory rats moved more vertically in a cubic maze, wild hummingbirds moved through the horizontal and vertical planes equally [44]. Furthermore, rats were more accurate in the horizontal than they were in the vertical plane, while hummingbirds were more accurate in the vertical rather than the horizontal plane. Differences in type of spatial cue used to solve spatial task the laboratory (e.g. proximal or distal cues) are also seen in cue use by wild hummingbirds. Here the explanation for the difference depends on spatial scale; not the kind of spatial scale that characterises pigeon homing or cuckoo migration but over distances of less than a metre. For example, hummingbirds remember which is the rewarded flower relative to other flowers within an array, but only when flowers are within 40 cm [45]. When flowers are further apart however, hummingbirds will use landmarks outside the array to choose the flower to visit [45,46].

Reconstruction of the search paths of trained, foraging hummingbirds shows that, when landmarks are made larger or are located further apart than they were during training, the hummingbirds' search locations are consistent with estimating distance and direction through view-matching [47,48]. This interpretation of the hummingbirds' use of visual information was only possible through the application of some technology,

specifically, analysis of videos captured by multiple cameras. The analysis component of these videos, however, was very far from high-tech: it involved extraction of x,y coordinates of the bird's location by hand from each video, a considerable amount of labour on the part of the first author of those papers. Unlike other recent papers in which comparisons have been made between laboratory and field performance on the same task [49], the data from these field experiments did not recapitulate data from birds trained to use landmarks in the laboratory. Rather, the view-matching of the birds more strongly resembles the way in which ants return to rewarding locations [50]. As has been noted previously [51], there have been few comparisons of cognitive performance between captive and wild populations, and where there have, there has been little agreement. In the hummingbird experiment, the question was not one of cognitive performance (i.e. better or worse) but what information the birds used to solve the spatial problem, and it seems more likely that spatial scale (already seen to be pertinent in the case of the hummingbirds) may explain the difference. Whatever the explanation, we might wish to be cautious about interpretations of variation in data that come from laboratory-field comparisons (cognition of the wild compared with cognition in the wild): such variation might have biological relevance. But it might also be one of context, and spatial scale is one very significant contextual difference between the laboratory and the wild.

One comparison with laboratory work for which spatial scale does not seem especially relevant is that of time-place learning, whereby animals learn when to visit one location rather than another. A very elegant laboratory study showed that garden warblers *Sylvia borin* not only learned which room to visit to gain food and when that room could be accessed, but that they learned to *predict* which of the four rooms to visit at the appropriate period through the day [52]. Like the garden warblers, rufous hummingbirds can also learn to use time of day to determine which patch of flowers is the most likely to contain food [53]. When the hummingbirds were trained with four patches of flowers, each patch of flowers rewarded for a different hour across four hours of each day, hummingbirds consistently chose the 'correct' patch for that time (Figure 1). Unlike the warblers, however, the hummingbirds did not seem to predict which patch to visit. Instead, they continued to visit a patch until they had evidence that further reward was not forthcoming in that patch (flowers when emptied did not refill). Upon encountering empty flowers, however, hummingbirds went directly to the patch that now contained food, as might be expected from a win-stay, lose-shift foraging strategy. This suggests that hummingbirds might not have learned circadian time in the way that the warblers appeared to have done, but had learned something about the sequence in which patches refilled. Such 'order' in which flowers refill, indeed appears to be important to the hummingbird sense

**Figure 1**
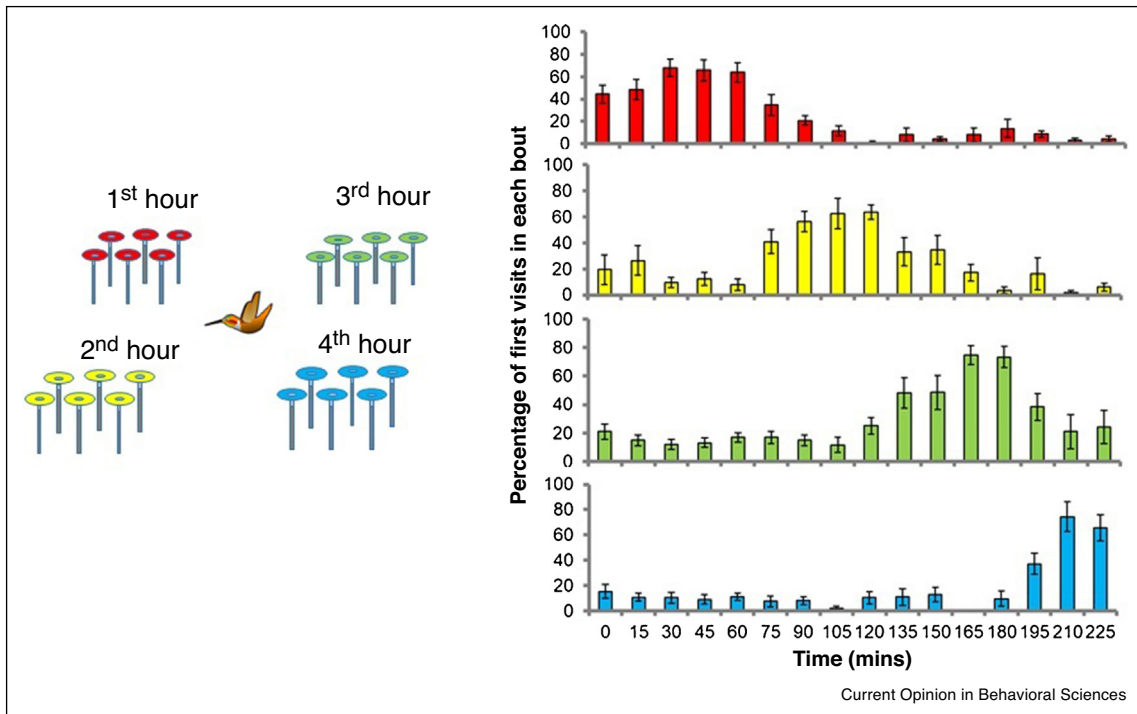


Left panel. Diagram of the flower array, showing four patches of six flowers. The flowers in each patch were the same colour, while patches differed in colour. Right panel. The percentage of first visits (mean ± S.E.) made by eight rufous hummingbirds to each patch over five days. Each of the four sets of coloured bars panel shows the visits made to each of the patches over the four hours. Modified from Ref. [53].

of time: in similar experiments where flowers were rewarded at specific times, hummingbirds used a combination of order and time of day to choose which of several flowers to visit [54]. In this coupling of spatial cognition with temporal cognition, we followed in the footsteps of a textbook example (episodic-like memory in scrub jays *Aphelocoma californica* [55]), subsequently leading to the discovery that these wild, free-living birds could remember what flowers to visit, where and when (see also Ref. [56]) and to evidence of numerical cognition [57,58••]. Among the questions raised by these data is how the hummingbirds integrate memories for multiple locations: do they use a 'simple' movement heuristic or construct a cognitive map of their surroundings?

### Take-home messages

The hummingbird research illustrates our take-home messages. By using modifications of classic experimental food-finding tasks we have, without the aid of technology, managed to uncover much about the spatial cognition that underpins foraging in wild, territorial hummingbirds. Just as for examining cognition in wild animals in the laboratory, our ability to collect high-quality data of appropriate quantity is hugely dependent on the logistic features of our chosen species. Features of these animals that have

enabled such examinations include the male's highly aggressive territoriality (other birds rarely get to visit the experimental arrays), the regular foraging trips (about every 10 min through the daylight hours), combined with the birds' profound indifference to the presence of humans (enabling observation from around 2 m) and their rapid learning of associations between stimuli (e.g. landmarks, colour) and reward. Much as we might like to examine cognition across a wide range of species in their natural environment, many animals live lives in locations that make such examination inordinately challenging [59].

Technology can also help us overcome some of the obstacles to testing cognition in wild animals (even for hummingbirds [60]) albeit only to a certain degree. Tracking devices have to be of an appropriate ratio of device/body weight that the animal has unimpeded movement and even so there is increasing evidence that carrying even lightweight devices can be costly. For example, in both the year of tagging and the following year, incubating Manx shearwaters *Puffinus puffinus* carrying GPS devices spent twice as much time away when foraging as did control birds, had a reduction in flight time of 14%, and gained 64% less mass per day [61••].

Using technology in the form of automated feeders where the animals come to the technology rather than wearing it has also become popular and these can be enormously profitable with regard to time spent training and in the amount of data collected in the absence of the researcher [62]. Indeed, devices of this kind have finally enabled work on food storing and spatial cognition to go back to the field, to cognition in the wild and not just of the wild. Indeed, this work is finally able to begin to determine the role that natural selection plays in spatial memory in food storers: no longer a key assumption, but access to testing that assumption. But such devices also have their drawbacks: they depend not just on birds learning how to manipulate the device, which may vary across individuals, birds must also return regularly.

Our final take-home message might appear equally as evident but a reminder will not hurt. In our enthusiasm for recent significant contributions to our understanding of spatial cognition in real animals in their real worlds, we have tried to point to older, key bases for the newer developments. Much as we encourage our students to keep up to date with the latest work in our field, and indeed, that is the aim of this issue (and explicit in the journal's title), we should also remind them not to disregard the older literature. While our recent technological advances are enabling us to address previously inaccessible questions, those questions are of the kind that arise from a mature field. They could not be addressed or even arise without the framework provided by very fine science conducted a decade or more ago.

## Conflict of interest statement
Nothing declared.

## Data availability
Data will be made available on request.

## Acknowledgements

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