DISPATCH

Animal Cognition: The Benefits of Remembering

Alex Thornton[1*] & Neeltje J. Boogert[1]

[1] Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, TR10 9FE, UK. E-mail: alex.thornton@exeter.ac.uk

How cognitive abilities evolve through natural selection is poorly understood. Two new studies show that a good spatial memory helps birds that hide their food to survive and produce more offspring.

Every morning, houses across the world are filled with the despairing refrain: “where have I left my keys?” We use our keys every day, yet we still manage to forget where we left them. Contrast this with a Clark’s nutcracker, which every winter hides over 30,000 seeds in locations across the forest and still manages to find most of them again several months later [1]. For such food-caching birds, it would seem obvious that being able to learn and remember locations must be advantageous, but until now direct evidence has been lacking. In fact, food-cachers have long been at the heart of acrimonious debates on the question of how cognition evolves [2,3]. Are animals cognitively specialised for the specific challenges they face in their environments, or is behaviour underpinned by the same general-purpose learning and memory mechanisms across species? Two papers in *Current Biology*, by Benjamin Sonnenberg and colleagues [4] and Rachael Shaw and colleagues [5] (this issue) shed light on this question, providing the first evidence that in wild, food-caching birds, individual variation in spatial memory is linked to survival and reproductive success and could therefore evolve through natural selection.

The last few decades have yielded more and more evidence for cognitive specialisations in food-caching animals. For instance, food-caching species typically have a larger hippocampus — the area of the brain associated with spatial cognition — than related non-caching species, and outperform non-cachers in some, but not all, experimental tests of spatial memory [3,6]. Similarly, in species of chickadee in North America, population-level differences in winter severity — and hence reliance on caching — are associated with pronounced differences in spatial cognition, hippocampal composition and neurogenesis [7]. However, whether these species- and population-level differences are generated by natural selection driving the evolution of genetically-based adaptive cognitive specialisations has remained an open question.

Building on their previous within-species comparisons in mountain chickadees (*Poecile gambeli*), Sonnenberg and colleagues [4] examined the potential for selection on spatial cognition in a high-elevation population of these birds in the Sierra Nevada that relies heavily on caching pine seeds over winter. They used an innovative experimental design in which birds fitted with miniature transponders had to learn and remember that only one out of an array of eight automated feeders would provide rewards (Figure 1). Adult birds made fewer mistakes than youngsters in their first year of life, consistent with the prediction that spatial memory helps birds survive their first winter, when mortality is particularly high. Individual birds' performance did not change across years, suggesting that the age difference in performance was not simply the result of differences in experience. Finally, in comparisons among first-year individuals, those that went on to survive the winter outperformed those that did not. Together, these findings provide compelling evidence that spatial memory could come under natural selection in mountain chickadees by promoting survival through winter.

To understand the action of selection, however, it is important to examine not only survival, but also reproductive success. Does greater spatial cognitive performance help individuals produce more offspring? Working with a wild population of New Zealand robins (*Petroica longipes*), Shaw and colleagues [5] suggest that the answer is 'yes'. Owing to the historical absence of predators in New Zealand, these birds are bold and curious, making it easy for the scientists to present individuals with a circular apparatus containing a series of eight wells, one of which was baited with food (Figure 1). As the apparatus was always placed in the same location and orientation, the birds could use spatial cues to remember which of the wells was filled with food. Among males, individuals that performed better produced more fledglings per clutch, and more of those survived until independence. These high-performing males also provisioned their offspring with a larger proportion of large prey items, but spent less time flying when provisioning chicks. Thus, increased foraging efficiency provides a potential mechanism through which spatial cognition could influence reproductive success. Interestingly, although female performance did not differ from that of males, females' success on the task was unrelated to their provisioning behaviour or reproductive success. The authors argue that this may be because females typically contribute less to offspring provisioning and rely less on food-caching (but see [8]) and suggest that differential selection between sexes could maintain variation in cognitive performance in the population. Sonnenberg and colleagues [4] make a related argument for mountain chickadees, where gene flow between high-altitude areas (where food caching is critical) and low-altitude areas (where caching is less important), could maintain variation in spatial cognition performance across the meta-population.

These two new studies [4,5] provide important evidence that selection is acting on spatial cognitive performance in food-caching species. What remains unclear is whether their findings reflect specific cognitive adaptations for food caching, or whether spatial cognition may provide similar fitness benefits in other contexts, or in non-caching species. In mountain chickadees, the suggestion that food caching is critical is supported by the finding that while spatial memory performance predicted subsequent survival, reversal-learning performance (a potential indicator of behavioural flexibility) did not [4]. Moreover, the fitness benefits of spatial memory appear to be specifically linked to over-winter survival, when caching is critical, and not to chick provisioning, which does not depend on caching [9]. Nevertheless, definitive evidence that local cognitive adaptations for food caching evolve via natural selection is still lacking [10,11]. In New Zealand robins, the evidence for cognitive adaptations specifically linked to food caching is less clear still. Indeed, Shaw and colleagues [5] suggest that the benefits of spatial cognition are associated with males' abilities to locate large, clumped food items with which to provision young, rather than the need to remember cache locations. In fact, it seems likely that good spatial memory could be beneficial for any species that forages on food that is predictably located in space. The specialisation on nectar-feeding in [OK?]hummingbirds, for example, has been linked to remarkable abilities to remember where rewarding flowers are located and the time it takes for nectar to replenish after being emptied [12].

However, it is not only foraging specialists that may benefit from a good spatial memory. For instance, in omnivorous striped mice from arid regions of Africa, males with better spatial memory are more likely to survive the summer drought [13]. In Australian magpies, another generalist species, individuals that perform well in tests of spatial memory also do well in other cognitive tasks, and high-scoring females have greater reproductive success [14]. This suggests that spatial memory may not come under selection in isolation, but rather as part of a cognitive package that allows individuals to respond appropriately to environmental variation across contexts. In previous work, Shaw and colleagues [15] have also shown that individual performance co-varies across a battery of cognitive tasks in New Zealand robins, although in that study the birds' spatial memory performance did not differ from random chance. Thus, whether selection acts specifically on spatial memory in this food-caching species remains to be determined.

Where do we go from here? Initial investigations of the links between cognitive performance and fitness in wild animals necessarily rely on correlational evidence, but further research may help to tease apart causal pathways and test adaptive hypotheses. For instance, developments in tracking technology may allow researchers to quantify the movements of individuals when caching and recovering food and link the efficiency of their behaviour explicitly to spatial memory performance in controlled experiments. Building on these new studies [4,5], researchers may now also begin to establish whether species or populations that rely more heavily on food caching experience stronger selection for spatial cognition than non-cachers. Further work could then combine experimental manipulations such as common-garden experiments [16] with genomic approaches to further disentangle genetic adaptations from environmental plasticity.

Research in animal cognition has traditionally been dominated by experimental studies in controlled laboratory conditions. In the last few years, a growing synthesis between behavioural ecology and cognitive psychology has led to an increased focus on the causes and consequences of individual cognitive differences in animals in their natural environments [17,18]. This approach is beginning to yield crucial evidence for the fitness consequences of individual cognitive variation across a range of different species and contexts. By linking cognitive tests to the challenges that animals face in the wild, we may unravel when evolution favours cognitive specialists, adapted to solve particular challenges like remembering cache locations, discriminating between group mates' faces [19] or inferring social relationships [20], versus cognitive jacks-of-all-trades.

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Figure 1. Testing spatial cognition in the wild.

Birds searching for food in experimental apparatus. Top: mountain chickadee, fitted with a transponder chip embedded in a violet colour ring (photo: Vladimir Pravosudov); bottom: New Zealand robin (photo: Rachael Shaw).