Spatial memory

The results of the field patch enrichment experiment were important in several ways. Theoretically, they provided a very clear, richly quantitative example of predicted responses, corroborating the theory. Others were seeing similar things in other systems, but the nature of hummingbird biology made our results easier to interpret. Unlike the case with most other animals, all hummingbird behaviour occurs in just a few metabolic modes, the costs of which are accurately known: hovering, flying forward, perching at some measurable temperature, and sleeping. Because we could see everything the birds did and had developed ways to record that behaviour accurately, our analysis of the economics could be unprecedented in its detail, helping to establish the hummingbird system as a model of territorial economics in general.

And for us, the implications of spatial memory were fascinating in terms of animal intelligence. How good ARE hummingbirds at learning spatial structure, anyway? When put to the test, how well can a 3-gram bird perform on a memory test? How much can they learn?

Glenn's masters' research on spatial memory asked how the geometric structure of foraging environments in the laboratory affects how quickly and how well hummingbirds learn them. Remember the revelation that had occurred to Stan Cook several years earlier in the same meadows, about the tight coupling of relationships in the hummingbird system? Glenn experienced something similar, and it similarly challenged his prior understanding of nature. Here is how I learned of it.

In the patch enrichment study, we observed from a tiny perch partway down from the lip of a 20-foot cliff, which afforded a perfect elevated view of the portion of meadow where we did our experiment. Because Glenn had grown up on a farm (I called him "the fair-haired boy from Saskatoon"), he preferred to record behaviour for the first 4 hours each day and I relieved him just before 10 AM. To observe continuously for 4 hours, recording each of 3000 behaviours to a small part of a second requires strong concentration, although the approximately 6-minute bouts of perching also afford time to think about things.

One morning, as I eased myself carefully-enough down the cliff to relieve Glenn without disturbing the birds in the meadow below us, he turned slowly toward me, much as Stan had done, and said, in a tone of voice I had not heard from him before, "They know what they are doing!"

A bit too flippantly, I replied, "Of course they know what they are doing. That's what we are studying and that's why we are doing the enrichment experiment."

Glenn replied, "But they know exactly where they are going before they go there, and except for when we play a trick on them, they know what they will find there. It's like they have a map of the whole meadow, and keep scribbling notes on the map to keep it updated with profitability, intruder pressure, and I don't know what else."

"What's the problem with that?"

Glenn said that the problem was that he had learned in an undergraduate course in animal behaviour that birds' nervous systems are too simple to allow learning and memory that sophisticated, and that what we were seeing in the meadow contradicted that belief. It wasn't that he didn't believe his own eyes, but that his prior knowledge had not prepared him to trust what he was seeing because it gave him no way to explain it. Part of what Glenn wanted me to know that morning was that he had decided to study spatial memory for his MSc research.

Here is how Glenn's spatial memory experiments worked in the laboratory.

A small room had a perch in the center and an 8 x 8 array of 64 identical feeders on one wall, separated from each other by about 10 cm. The array was covered by a window blind, which was out of the way of the feeders for only one minute out of every 10. Half of the feeders provided food and the other half were always empty, and the bird's problem was to learn which were which. There was enough time to visit all 32 good feeders in a minute, but not to visit all 64 good and bad ones. The 32 good feeders supplied all the food the bird would get for most of a day. These conditions motivated the hummingbirds to attend carefully to the problem.

The basic result was that hummingbirds learned simply-structured environments much faster than they did complex ones, reinforcing the idea that geometric structure is important in spatial memory. They did not learn the details independently, but learned the way the details related to each other spatially: spatial pattern. But with enough time, they learned complex patterns just as well as simple ones, and used them just as profitably. The most complex patterns were really difficult for us to learn, yet 3-gram hummingbirds learned them just fine with enough practice.

An experimental trick we called the "switch experiment" reinforced our sense that in nature, hummingbirds forage by spatially structured expectations based on spatial memory. That is, they develop a "map" of the distribution of profitability in their environments, then forage as if that map were accurate. To test this idea, the switch experiment threw a monkey wrench in the expectation. Here's how it worked.

Glenn allowed individuals to learn each of the four patterns, and then switched the patterns to their mirror images between trials (without telling the birds). All feeders that had been good before the switch were suddenly bad, and vice versa. If the birds had been foraging by expectation just before the switch, say making 90% of their visits to good feeders, then the switch should throw them down to only 10% success. But if their success before the switch resulted from something other than spatial memory (there are several possibilities), they should continue at a high level without being thrown off by the switch.

In every case including the most difficult patterns, the switch threw them for a loop, confirming the notion that they were foraging by expectation. Later, Gord McIntyre showed that the longer the pattern is stable before the switch and the better the hummingbirds are at foraging in it, the longer they persist in the same unprofitable behaviour after the switch, the less food they get, and the more body weight they lose before learning the new pattern. Experience of success in foraging by expectation before the switch breeds resistance to change after the switch. It was like looking in the mirror for us to see 3-gram hummingbirds behaving as if they knew what was going on, when clearly they didn't!