MEMORY IN FOOD-HOARDING BIRDS

by Harriet E. Hoffman, Arlington

The presence of food-hoarding behavior in a number of species of birds is known to many of us. Almost everyone has observed birds fly to a feeder, take a seed, fly away, and return almost immediately for another. Common sense would suggest that the birds could not possibly be eating the seeds in the short interval between return trips to the feeder. Therefore, they must be storing the seeds for future use, be it hours, days, or months later. The extent to which memory is involved in aiding the birds to retrieve their caches is perhaps not so well-known.

How do birds find the food they have stored? Do they rely on memory? If so, they would need a capacious and long-lasting memory. In principle, birds could find their food stores without memory. They could always use the same type of site and then search by trial and error or use a cue such as odor. Behavioral psychologists are becoming increasingly aware that animals do have a capacity for memory: birds remember songs, and bees remember flowers. Birds that can remember where they stored food would make fewer errors in search and hence expend less time and energy than birds that relied on trial and error. Thus, the development of memory would have distinct survival value for food-hoarding birds. Birds that hoarded in times of plenty and that could remember the location of their caches would be able to draw on their hidden supplies in lean times. As a result, they would live to reproduce, and nonhoarders would be less successful.

Memory in birds is being tested in both field and laboratory experiments with the Marsh Tit (Parus palustris), a European relative of the Black-capped Chickadee, and Clark's Nutcracker (Nucifraga columbiana). An article by Sara Shettleworth (1983), reported on research on the memory capacity of birds conducted by John Krebs, Richard J. Cowie, David F. Sherry, Mark Avery, Allen Stevens, and Shettleworth at the University of Oxford; Diana Tomback, University of Denver; and Stephen B. Vander Wall, Utah State Univeristy. Vander Wall's (1983) field research on Clark's Nutcracker has also recently been reported in Natural History.

In England all that is needed to show the remarkable memory powers of Marsh Tits is a birdfeeder stocked with peanuts. Observation shows that Great and Blue tits will remain at the feeder and eat as fast as possible, whereas a Marsh Tit will dart in, snatch a peanut, fly off, only to return again and again until the supply is exhausted. It stores the peanuts at different sites, and then returns to eat them later. A Clark's Nutcracker will behave similarly. In the late summer it harvests the seeds of Piñon Pines, fills its sublingual

pouch, and flies several miles to bury them, often on southern slopes, where the snow is not so deep in winter. It may bury as many as 33,000 seeds in a cache and return to dig up thousands of caches throughout the winter.

In field experiments in Wytham Wood near Oxford, Krebs and his co-workers put out dispensers of sunflower seeds and trained Marsh Tits to come to the dispensers. The husks of the seeds (removed by the birds before eating) were coated with a radioactive substance, which permitted frequent checking of the tits' storage sites to determine when the hoards were used up. The investigators set up false hoards of seeds as controls, each located one meter from a hoarding site made by a bird. If Marsh Tit memory were involved in finding and depleting the caches, the birds' natural hoards (seeds with radioactive husks) should disappear faster than the control hoards, and they did. However, because predation of the stored seeds by rodents and other birds is common, the control caches set up by the experimenters lasted only a day or so longer than did the caches established by the Marsh Tits.

To eliminate the effect of this predation factor, Krebs next conducted experiments in the laboratory. First, Krebs, Sherry, and Cowie offered the tits bowls of sunflower seeds to eat and trays of moss in which to hide the seed. Second, Krebs and Shettleworth offered the birds hempseed to eat and store and tree branches with approximately 100 holes (each could hold only one seed) in which to hide the seeds. In one of the initial experiments a Marsh Tit was permitted to store twelve seeds taken from a bowl in the middle of the room. When all twelve were stored in twelve different holes, the bird and the bowl of seeds were removed from the room for two and a half hours. Then the bird was put back in the room and was allowed to search for seeds. If the bird searched at random, it would require visits to about eight holes to find one seed. The tit was actually more efficient. The average was about two mistakes per seed. At the beginning of the recovery test, a tit often was able to recover three or four seeds before encountering an empty hole.

The researchers then put the birds through a progressively more specialized series of remarkably inventive experiments designed to show that the Marsh Tits were indeed using memory to find the hidden seeds. Specific results are as follows. It was possible to eliminate "recency effect" (most recently hidden seeds would be remembered first); the possibility of odor as a cue was eliminated; the tits when storing seeds avoided sites they had already used; and they apparently processed two kinds of information: they remembered where the food was, and they remembered where they had looked.

Experiments with Clark's Nutcracker both in the field and in the laboratory have elicited further proof of spatial memory.

In a field experiment Tomback was able to record the number of successful and unsuccessful searches of nutcrackers in the snow because they leave visible beak marks and piñon seedcoats next to the holes. If the searches were random, the number of successful and unsuccessful probes should be equal. In reality, two thirds of the probes were successful. In the laboratory Vander Wall conducted experiments with four Clark's Nutcrackers, two of which were hoarders, and two nonhoarders. The hoarders retrieved food successfully in 70 percent of the probes, whereas the nonhoarders had a success rate of only 10 percent. Through a progression of experiments he showed that the hoarding birds used objects, for example, logs and rocks, as cues for remembering storage sites, and both hoarders and nonhoarders searched most often near such objects.

Do food-storing species have better memories than nonstorers? Tests on food-storing birds using nonfood objects have not yet been done. A close relative of the type of experiment that would be needed is a delayed-response experiment. In it an animal is shown visual cues, such as flashing lights or a geometric shape. It is later given a choice between the original object and another. It is rewarded if it chooses the first. When pigeons, i.e., nonfood hoarders, were given this sort of test, with a food pellet as a reward, they did not succeed.

What birds are known to store food? The Acorn Woodpeckers of our western states may store as many as 50,000 acorns in one tree. In New England, nuthatches and titmice store insects and seeds in bark crevices, and in Europe, other Paridae, the Willow and Crested tits, store in the fall and draw on caches over the winter. In Norway, the latter stores food on the under side of branches where it is available even after heavy snowfall. The Marsh Tits of Europe store for short periods; the Blue and Great tits do not. The Clark's Nutcracker makes use of communal caches whereas the Scrub Jay caches only in its own territory. The nutcrackers of Sweden spend three months of autumn storing hazelnuts and flying as far as six kilometers to bury nuts in small heaps covered with moss and lichen, chiefly in spruce forests. They then retrieve them in winter and spring, sometimes from snow as deep as forty-five centimeters with a success rate of 86 percent. Jays of different species, including our Blue Jay, hide food in crevices and holes in the ground. The Piñon and Steller's jays are only moderate food-hoarders, and more observation and research are needed. Experiments with captive ravens (Corvus corax) demonstrate that the hungrier the bird, the more food it hoards. (Welty, 1982:128 and Shettleworth, 1983).

Shettleworth has written an understandable and stimulating article. I was impressed by the ability of food-hoarding birds to remember where they hid their caches. I was even more impressed by the scientists who devised the extraordinarily creative laboratory and field experiments to prove that some species of birds possess the capacity for spatial memory.

REFERENCES

Shettleworth, Sara J. 1983. Memory in food-hoarding birds. Scientific American 248 (March): 102-110.

Vander Wall, Stephen B. and Russell P. Balda. 1983. Remembrance of seeds stashed. Natural History 92: 60-65.

Welty, J. Carl. 1982. The Life of Birds, Third Ed. CBC College Publishing.

HARRIET E. HOFFMAN is Assistant Editor of the Quarterly Journal of Economics at Harvard University and a member of BOEM's editorial board. Although she majored in history at Grinnell College and became an editor by profession, an early interest in birds developed from observing a Pileated Woodpecker gouging away at a tree outside the family's summer home in Connecticut. Dr. Paynter's course in ornithology at Harvard and a 1975 whale-watching trip off Baja California intensified and expanded this interest to include marine mammals and led to an enduring enthusiasm for pelagic trips.

NORTH CAROLINA GULF STREAM PELAGIC TRIPS

On May 27, July 29, September 1, September 2, and October 7, 1984 there will be pelagic birding trips into the Gulf Stream off North Carolina's Outer Banks. These trips, which leave from Hatteras, are famous because of the expected specialities such as Black-capped Petrel, Audubon's Shearwater and Bridled Tern. For complete information on the trips, please contact the leaders: Robert L. Ake (615 Carolina Avenue, Norfolk, VA 23508; phone 804-625-6082, evenings to 11 P.M.) or Paul G. DuMont (4114 Fessenden Street, NW, Washington, D.C. 20016; phone 202-363-8994, evenings to 11 P.M.) The trips are $48 per person per trip.