LAYING RED-COCKADED WOODPECKERS CACHE BONE FRAGMENTS'

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Birds rely largely on dietary calcium to produce eggs because they have limited calcium reserves (see Gilbert 1983). Diets consisting of fish and shellfish may contain sufficient amounts of calcium for egg production (Gilbert 1983), but insects (Turner 1982) and seeds and foliage (Scott et al. 1976, Gilbert 1983) contain too little calcium to maintain observed rates of laying. Swallows (Hirundo rustica), for example, lay one egg per day, and they have about 16 hr of daylight for foraging. Yet, on a diet of insects they would have to forage for 12 to 36 hr, depending on the weather, to obtain enough calcium for a single egg (Turner 1982). Laying hens, which produce eggs even while on lowcalcium diets, adjust their laying rates so that the amount of calcium output in eggs and urine matches input from the diet (Gilbert et al. 1981). Calcium deficient diets result in reduced eggshell thickness (Gilbert et al. 1981), reduced clutch size (Dale 1955, Greeley 1962, Chambers et al. 1966, Krapu and Swanson 1975), and reduced hatching rates (Krapu and Swanson 1975). Typical rates of egg production are maintained by increasing calcium input. Reproductive hens can absorb calcium from the digestive tract more efficiently than non-reproductive hens, and they increase the amount of calcium in their diet on laying days (see Gilbert 1983). Depending on what is available, they increase calcium intake by eating more food, more calcium-rich foods, and calcareous grit (see Gilbert 1983).

Wild birds also increase the amount of calcium in their diets during the laying period. Among studies of food habits, it is commonly observed that bone fragments (MacLean 1974), mollusk shell (Jones 1976, Davies 1977, Beasom and Pattee 1978, Ankney and Scott 1980) and calcareous grit (March and Sadleir 1972, Jones 1976) appear in the diets of birds during the breeding season whereas they are less common or absent at other times of the year. Detailed information indicates that intake of supplemental calcium is closely Little is known about how wild birds actually obtain calcium for egg production. They may be able to ac-

associated with laying (Jones 1976, Beasom and Pattee

1978, Ankney and Scott 1980).

quire it incidentally during other activities if the source is abundant and widespread, or they may have to expend considerable effort to obtain it if it is rare or localized. Both situations probably occur. For example, MacLean (1974) observed that raptor pellets, the most likely source of calcium for the arctic sandpipers (*Calidris* spp.) that he studied, were extremely abundant. Band-tailed Pigeons (*Columbia fasciata*), on the other hand, congregate at mineral springs during a discrete portion of the breeding season to obtain salt-coated gravel (March and Sadleir 1972), suggesting that individual birds move quite some distance to obtain supplemental calcium. The swallows studied by Turner (1982) spent about 30 minutes per day obtaining calcareous grit.

We report here anecdotal observations of breeding female Red-cockaded Woodpeckers (Picoides borealis) obtaining and caching bone fragments. Although sources of calcium were available within the home ranges of the birds that we studied, they were not abundant, and individual birds made distinct moves to go to them. That the birds cached bone fragments was particularly interesting because it appears to be in discordance with the usual adaptive explanations of food caching: stockpiling resources for periods of extreme need, forestalling the natural decline of a resource, and garnering time for activities other than foraging (see Sherry 1985, Vander Wall 1990). We suggest that bone fragments were cached for more immediate benefits resulting from the economics of handling individual pieces. These circumstances are similar to those in which food caching might have originated.

METHODS

Our observations were collected during two, year-round studies of the home range of Red-cockaded Woodpeckers in the Sandhills of south-central North Carolina. During the egg-laying season, one breeding pair of birds was tracked for five days by Repasky in 1980, and three breeding pairs were tracked for two days each by Blue in 1981. Although non-breeding helpers are sometimes associated with breeding pairs of Red-cockaded Woodpeckers (Ligon 1970), the breeding pairs that we studied lacked helpers. Tracking was carried out by following a pair from dawn to dusk. We plotted the location on an aerial photograph and recorded a scan sample of behavior (foraging, resting, territorial conflict etc.) at 5-min intervals. We included eating or handling of bone fragments as a behavior once it became apparent. Further details of our tracking methods

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and study areas are reported by Repasky (1984) and Blue (1985). The date on which laying began was known for the female tracked by Repasky. Clutch initiation dates for the females tracked by Blue were estimated from the nest check records of Carter et al. (1983) and Walters et al. (1988). Hatching dates were back calculated from the estimated age of nestlings when they were first observed, and incubation was assumed to be 11 days (see Walters et al. 1988).

To determine whether females encountered bone fragments incidentally while they foraged or whether they went out of their way to acquire fragments, we compared the distances moved by individual breeding pairs of birds during the 5-min period in which they arrived at a source of bone fragments to the average distance moved in 5 min. Randomization tests (Edgington 1987) were used to make the comparisons because successive movements were not independent of one another. If we observed n arrivals, 999 random samples of the distance moved in 5 min, each of size n, were drawn from the set of all distances moved during the five-day or two-day tracking period. The set of arrival distances was added as the thousandth sample. Finally, the likelihood that the set of arrival distances was a random sample of distances moved was calculated as the proportion of sample means at least as large as the one observed. We report the means, ranges and probabilities. Standard deviations of the distances moved are omitted because they are badly biased by the lack of independence.

RESULTS AND DISCUSSION

We observed two of the three females that we tracked near the time of egg laying make use of supplemental calcium. One of the females was tracked from three days before egg laying through the second day of laying. The other was tracked on approximately days six and eight prior to beginning her clutch. One of the females that we did not observe make use of supplemental calcium was tracked on days 18 and 19 prior to clutch initiation, and the other was tracked during the incubation period.

The females took bone fragments from raptor pellets located on the ground. They approached pellets in several ways: they would fly directly to the pellet, land nearby and hop to the pellet, or, if the pellet was near a tree, hitch down the trunk of a tree to the ground and then hop to the pellet. Small bone fragments were consumed at the pellets whereas larger pieces were taken to a tree trunk (by flight) where they were pecked and mandibulated. Unfortunately, it was never possible to determine how much, if any, of a piece of bone was consumed. Pieces of bone were cached by placing them between scales of bark and then hammering them with the bill until they were wedged. We confirmed that bones were cached by recovering two pieces of bone from trees and by observing birds recover cached bones, handle them and cache them elsewhere.

Encounters with raptor pellets were not incidental to other activities even though they were located well within known home range boundaries. Visits to pellets occurred in the afternoon: 18 of 19 visits began after 14:30. Within home ranges, the only pellets that we knew of were those used by the birds, although we did not actively search for others. The average distance moved during the 5-min period prior to visiting a pellet was greater than the average distance moved during all 5-min intervals (first breeding pair: 110 m moved to pellet [n = 13, range 0 m to 300 m], 40 m moved in average 5-min interval [n = 607], range 0 m to 360 m, P = 0.001; second breeding pair: 85 m moved to pellet [n = 6, range 20 m to 150 m], 41 m moved in average 5-min interval [n = 282], range 0 m to 390 m, P = 0.027) suggesting that birds altered their movement patterns to obtain supplemental calcium.

We also observed behaviors that we believe may be used to locate calcium sources. Blue observed a female fly to the ground repeatedly to investigate white pieces of paper, and Repasky, on several occasions, observed a female hitch backward down to the base of a tree and then hop between trees while searching the ground. These behaviors were not observed at any other time during the year. Outside of the breeding season, we rarely observed woodpeckers on the ground, but when we did the birds were drinking, bathing or eating the fruits of low-growing plants (e.g., *Gaylussacia dumosa, Rhus toxicodendron*).

So far as we now, this is the first report of a bird caching a food for which the primary value is mineral rather than caloric.

None of the three fitness advantages usually attributed to food storing seems to be a satisfactory explanation of bone caching by Red-cockaded Woodpeckers. Caching is thought to increase fitness when: 1) stored food mitigates the effects of declining food abundance; 2) stored food ameliorates the effects of sudden periods in which the need for food is unusually high; and 3) stored food frees the animal from searching for food at some later time when fitness can be increased by allocating time to other tasks (Sherry 1985, Vander Wall 1990). Raptor pellets are unlikely to be a resource that is declining in abundance. Neither the abundance of pellets nor the life span of individual pellets appears to be ephemeral. Pellets might be depleted competitively by other species using calcium, especially rodents, although there is not a literature on the subject. The rate of depletion would have to be enormous because use of supplemental calcium is restricted to the egg-laying period (Jones 1976, Beasom and Pattee 1978, Ankney and Scott 1980). In fact, the pellet used by the female observed by Repasky was still present two months after the female made use of it. Red-cockaded Woodpeckers rear only one brood per year so bone caches do not forestall depletion that might occur between broods. It is also unlikely that cached bone fragments buffer females from periods in which their need for calcium is extremely high. The advantage of cached food is that the animal does not have to search for food during the period of need. A delay between the time food is stored and the time of need is absent for the woodpeckers: they cache bone fragments only during the period of need. Furthermore, the cost of search is minimal because the birds knew the locations of pellets. Individual females returned to the same pellet several times per day on successive days. Alternatively, the nestling stage could be a period of increased need for dietary calcium if nestlings require large amounts of calcium for growth. However, we tracked three family groups during the nestling stage and failed to observe birds collecting bone fragments. Finally, the same arguments against stores for periods of extreme need apply against stores freeing time for activities other than acquiring bone fragments. The requisite time delay between gathering and use is absent, and search time is already minimal.

Food storing may occur when food items can be only partially consumed and a fitness advantage can be gained by returning to previously captured food items. The advantage is not contingent upon some future change in need, food abundance or time demands; those factors may remain constant. It stems solely from the benefit of returning to an individual food item. In the case of Red-cockaded Woodpeckers, large bone fragments are carried up into trees. The fragments are too large to be consumed at once, and the bird has the choice of discarding them or caching them and returning later. The advantage of caching might be in the time saved and/or in minimizing the risk of predation incurred while acquiring another fragment. Indeed, the hazard of avian predation to arboreal passerines is least in tops of trees and increases toward the ground (Ekman 1986, Hogstad 1988). Risk to ground-feeding passerines increases with increasing distance from cover (Caraco et al. 1980). Hence, a trip to the ground might be particularly hazardous to a woodpecker.

If our assessment is correct, the bone caching by Redcockaded Woodpeckers is primitive. The conditions in which it occurs are similar to those under which caching is thought to have evolved, and the advantage is independent of future changes in need or resources. Richards (1958) suggested that carrying food to a handling site may represent the initial stage in the evolution of food caching, and caching behavior appears to be restricted to taxa that do so (Sherry 1985). The handling site might be a suitable substrate for handling the food item (Richards 1958) or a site safe from predators (Turcek and Kelso 1968, Lima 1985). Both of these are plausible explanations of why Red-cockaded Woodpeckers carry large pieces of bone to trees for handling. It is probably from simple conditions such as these (see Vander Wall 1990 for others) and an immediate advantage to caching that more complex forms of caching evolved. We suspect that other taxa may also cache food for immediate benefit under equally simple conditions. For example, large carnivores sometimes kill prey much larger than they can consume at once. Turcek and Kelso (1968) and Macdonald (1976) have suggested that large prey result in caching, but the immediate payoff of doing so has been overlooked.

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ASH-THROATED FLYCATCHERS (MYIARCHUS CINERASCENS) RAISE MOUNTAIN BLUEBIRD (SIALIA CURRUCOIDES) YOUNG¹

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Key words: Facultative brood parasitism; nest site competition; Myiarchus cinerascens; Sialia currucoides.

Ash-throated Flycatchers (*Myiarchus cinerascens*) and Mountain Bluebirds (*Sialia currucoides*) are secondary cavity-nesters that are sympatric in juniper woodlands of northern Nevada. While conducting a study of Mountain Bluebird reproductive strategies during the 1988–1989 breeding seasons, we observed two instances of Ash-throated Flycatchers raising bluebird nestlings in addition to their own young.

Our study area is located in partially burned juniper woodlands north of Reno, Nevada, and contains 68 nestboxes. These boxes have been used since 1985 by Mountain Bluebirds and are also used occasionally by Ash-throated Flycatchers.

In the first incident, a nestbox which contained two bluebird eggs on 30 May 1989 was taken over by Ashthroated Flycatchers. The adult bluebirds were unbanded, so we are not sure what happened to them after losing the nestbox; they did not use the nestbox again that season. The female flycatcher did little additional nestbuilding (flycatchers in this area use clumps of fur for nest material whereas bluebirds mainly use strips of bark), but laid her clutch of five eggs alongside the two bluebird eggs by 6 June. She incubated the mixed clutch, and all seven eggs hatched on approximately 19 June. In the four times we checked the nest between hatching and 3 July, the rate of nestling development appeared to be equal for both species. Only flycatchers were seen feeding the young. All nestlings presumably fledged on 11 July, except for one almost completely feathered bluebird nestling found mummified in the nestbox on 12 July (cause of death unknown). Despite repeated searches, we did not see the young after fledging.

In the second incident, an Ash-throated Flycatcher laid two eggs by 22 June 1989 in a nestbox in which a bluebird pair had previously fledged a clutch of four young. On 5 July there was one Mountain Bluebird egg in the nest, along with two additional Ash-throated Flycatcher eggs. The flycatcher incubated all five eggs. On 12 July, we found one bluebird and two flycatcher young along with a dead flycatcher nestling and an unhatched egg. The young were approximately two days old. Again, only flycatchers were seen caring for the young. On 15 July (five days after hatching), the nest contained only two dead young (one flycatcher and one bluebird). The other nestling and the unhatched egg were missing. The adults were not in the area and were not seen again. Since predation is a major cause of bluebird egg and nestling mortality in our study area (unpubl. data), we assume this was the cause of nest failure, though nest abandonment cannot be completely ruled out.

To our knowledge, this is the first report of Ashthroated Flycatchers raising the young of any other species. These two cases are qualitatively different, and we consider two possible explanations for them: 1. competition for suitable nest sites, and 2. facultative brood parasitism.

Nest site competition. Two lines of evidence suggest that Mountain Bluebirds and Ash-throated Flycatchers compete for suitable nest sites in this study area. First, we know of four takeovers of bluebird nests by flycatchers since 1985 (two in 1986, one in 1987, one in 1989). There have been no reciprocal takeovers by bluebirds, presumably because flycatchers are much

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