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A NESTING HUMMINGBIRD FEEDING SOLELY ON ARTHROPODS

ROBERT D. MONTGOMERIE

AND

CATHERINE A. REDSELL

Hummingbirds usually forage on floral nectar and other sugar sources, apparently feeding on insects and other arthropods only incidentally (Feinsinger and Colwell 1978). Although Wagner (1946) and others have suggested that some species feed largely on insects at certain times of the year, detailed time budget studies of various hummingbirds have shown that less than 15% (and usually less than 5%) of their foraging time is spent catching arthropods (for summary, see Gass and Montgomerie 1980). Even during the nesting period, when animal food may be nutritionally important for egg production and nestling growth (Ricklefs 1974), female hummingbirds seem to rely on nectar as their primary energy source (Hainsworth 1977). Here we present evidence that a nesting hummingbird can subsist, at least for a few days, on a diet of arthropods.

During the last two weeks of May 1978, we observed a nesting female Broad-tailed Hummingbird (*Selasphorus platycercus*) in Rose Canyon, Santa Catalina Mountains, Arizona (elev. 2,200 m). The nest was 3.9 m up in a silverleaf oak (*Quercus hypoleucoides*) in an open woods of oak and ponderosa pine (*Pinus ponder-*

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Division of Biological Sciences, The University of Michigan, Ann Arbor, Michigan 48109. Present address: Department of Developmental and Cell Biology, University of California, Irvine, California 92717. Accepted for publication 29 April 1980.

osa), and contained two eggs on both 21 and 31 May. We recorded time budgets of the female on 19, 20, and 21 May by sampling for a randomly chosen 10-min period during each daylight hour (06:00 to 20:00). Time spent by the bird in each activity was recorded to the nearest 2 s. We were able to keep the bird in sight for 91% of the 520 min of observation. We always began an observation from a location about 15 m from the nest, far enough away that the incubating female did not appear to be disturbed by our presence.

We began this study because the extensive woodland habitat around the nest lacked the nectar-producing flowers that hummingbirds usually visit. To measure this, we surveyed a transect 500 m long by 30 m wide along each of the eight cardinal compass directions away from the nest. These covered about 15% of the 1-km diameter circle centered on the nest. During 19–22 May we found only a few Viola, Helianthus, and Potentilla flowers within this area, and none of these produced measurable quantities of nectar. On 31 May, however, Indian paintbrush (Castilleja miniata) was common. Three inflorescences were blooming less than 50 m from the nest and all contained nectar.

During the 19 foraging bouts (totaling 1,150 s) that we observed, the hummingbird spent all of her time either flycatching, gleaning from leaves, probing among lichens on tree trunks, or flying between foraging sites. Most of these observations were made within 100 m of the nest, but twice we followed her about 400 m up a small stream where she caught flies above a pool. Although we were able to follow this bird only 22% of the time that she was off her nest, most of these bouts were brief ($\bar{x} = 113$ s, SE = 18.7, n = 62), and the bird was often audible as she foraged

in dense foliage nearby. Thus, we are confident that this hummingbird foraged mainly within the 1-km circle that we censused for flowers. No nectar-producing plants bloomed within this area until *Castilleja* appeared on 31 May, so the bird must have subsisted only on arthropods for at least two weeks.

Of the time that the female was in sight while off the nest, she spent 76% of the time foraging and 24% gathering nest lining or working on the nest. She was off the nest for 28% of the time observed (range 14–38%, n = 3 days). This proportion is similar to those of other incubating hummingbirds (i.e., average 24% of daylight spent off the nest; four studies of three species; Calder 1974), even though these other species spent most of their time foraging on nectar. Our observations are consistent with Hainsworth's (1977) analysis that indicated the Sparkling Violetear (Colibri coruscans) was able to forage as efficiently on insects as on nectar.

Could this hummingbird have obtained sufficient nourishment by feeding only on arthropods? From a general equation for daily energy expenditure in birds (King 1974:39), we estimated that this bird spent about 26 kJ per day (assuming 3.8 g body mass; Kodric-Brown and Brown 1978). To estimate the energy content of her food, we caught flies from a swarm where the female had been flycatching. The average dry weight of a fly was 2.1 mg (SE = 0.10, n = 15) and each would have yielded about 32 J of metabolizable energy (Ricklefs 1974:157). Thus, to balance its daily energy budget the hummingbird would have needed to catch about 800 flies, or about five flies/min, during all of its daily foraging time. Our casual observations, and Hainsworth's (1977) data, indicate that this rate of capture is well within a hummingbird's abilities. Our estimate is obviously crude because this bird caught other kinds of arthropods and we have no information on its complete diet. It shows, nonetheless, that a hummingbird can obtain enough energy without floral nectar.

Given the 14-day incubation period of Broad-tailed Hummingbirds (Bent 1940), the eggs in this nest should have hatched during the first few days of June, right after Castilleja began to bloom. The nest timing of this female was, therefore, virtually identical to that of Broad-tailed Hummingbirds near Gothic, Colorado, where hatching was timed to occur after the major nectar-producing plants (C. miniata and Ipomopsis aggregata) began to flower (Waser 1976). In Colorado, the birds apparently feed on the nectar of Delphinium nelsoni during incubation, but the results of our study indicate that such precise nest timing can occur even when no nectar-producing flowers are available before the eggs hatch.

This study raises the question: why don't more hummingbirds subsist on a diet of arthropods? The most probable answer is that nectar is energetically more profitable than arthropods, largely because its distribution, abundance, and food quality are predictable in both space and time; therefore, foraging time can be minimized. Arthropods should be most profitable: (1)

when they are clumped and abundant (e.g., swarms of insects in willows defended by Rufous Hummingbirds, Selasphorus rufus; K. Lertzman and C. L. Gass, unpubl. data); (2) when they are renewable in predictable locations (e.g., arthropods stolen from spider webs by tropical hummingbirds; Young 1971); (3) when they are nutritionally important (e.g., for nestling development; Hainsworth 1977); and (4) when nectar is unavailable (e.g., present study). We suggest that observations of hummingbirds in each of these situations will reveal more feeding on arthropods than has been previously recorded.

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Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1. Present address: Department of Biology, Queen's University, Kingston, Ontario, Canada K7L 3N6. Accepted for publication 8 May 1980.