

## SHORT COMMUNICATIONS

*The Condor* 90:233-236  
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### DIFFERENT FEEDING STRATEGIES OF TWO SYMPATRIC HUMMINGBIRD SPECIES<sup>1</sup>

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**Key words:** Rufous Hummingbird; *Selasphorus rufus*; Calliope Hummingbird; *Stellula calliope*; competition; foraging strategy; territoriality; *Castilleja miniata*.

Most North American hummingbird species are separated from one another during the breeding season by different habitat preferences. In migration, however, different species often share the same habitat. Migrating hummingbirds are usually aggressive and often territorial both inter- and intraspecifically (Armitage 1955; Cody 1968; Dunford and Dunford 1972, pers. observ.). This was the case on Wheeler Peak in eastern Nevada, where Rufous Hummingbirds (*Selasphorus rufus*) and Calliope Hummingbirds (*Stellula calliope*) shared the same habitat and food source. The purpose of this paper is to describe some differences in the means by which these two species exploited the food resource.

#### STUDY AREA AND METHODS

The hummingbirds were observed on Wheeler Peak, White Pine County, Nevada, 39°00'30"N, 119°19'30"W. The study area was an east-facing slope of about 35°, approximately 2.5 km long (north-south) by 1 km wide (east-west).

Vegetation on the hillside formed roughly three levels: the uppermost consisting of scattered limber pine (*Pinus flexilis*) and Englemann spruce (*Picea engelmanni*) both to about 20 m tall; the next composed of thickets of quaking aspen (*Populus tremuloides*) to about 4 m tall; and the lowest consisting of *Juniperus occidentalis* (widely scattered) and a few species of herbaceous flowering plants, notably *Castilleja miniata*, *Monardella odoratissima*, and *Penstemon leiophyllus*. The composition of the floral resource available to hummingbirds was roughly 70% *C. miniata*, 20% *M. odoratissima*, 9% *P. leiophyllus*, and 1% *Silene douglasii* and other species. The substrate was primarily limestone talus, pieces averaging about 1 dm<sup>3</sup>.

I observed the birds every day from 11 July to 27 July 1985, inclusive, from about 06:00 to noon, and

13:30 to 18:00. During these periods I observed hummingbirds for a total of about 90 hr.

To determine feeding rate I used a stopwatch. Upon sighting a feeding hummingbird, I simultaneously started the stopwatch and began counting probes the bird made into the flowers. When the bird either stopped feeding or was lost from sight I stopped the stopwatch and noted the number of probes per elapsed time. This process was repeated with several different hummingbirds of both species. Feeding heights were estimated using reference stakes 0.5 m tall and marked at 0.1-m intervals, placed at the edges of *Castilleja* clumps commonly used by feeding hummingbirds. As a hummingbird fed within the clump each probe was recorded in the appropriate height category: 0-10 cm, 10-20 cm, 20-30 cm, 30-40 cm, or 40-50 cm until the bird either stopped feeding or was lost from sight. This process was repeated in several clumps of flowers and with different hummingbirds of both species.

For statistical analysis, the hummingbirds were divided into eight groups: male Calliope, female Calliope, male Rufous, female Rufous, all Calliope, all Rufous, all males, and all females. *T*-tests were used to compare the feeding rates of the eight groups.

Assuming that hummingbirds feeding at random with respect to height would make equal numbers of probes in all categories, I used  $\chi^2$  tests to determine whether or not each group selected flowers of any height category.

In comparing heights of the different hummingbird groups to each other, expected values were determined for each group in each height category by multiplying the number of probes made by both groups in that height category by the proportion made by that group of the total probes. The eight groups were all compared to each other using  $\chi^2$  tests.

#### RESULTS

Despite the presence of other flowers, the hummingbirds of Wheeler Peak fed almost exclusively on *Castilleja miniata*. In the entire observation period I saw hummingbirds feed on other plants only three times: Calliope and Rufous once each on *Penstemon leiophyllus*, and Calliope on *Monardella odoratissima*. All observed feeding bouts on flowers other than *C. miniata* lasted less than 10 sec.

<sup>1</sup> Received 1 August 1987. Final acceptance 2 October 1987.

TABLE 1. Feeding rate of Calliope and Rufous hummingbirds at Wheeler Peak, White Pine County, Nevada.

	No. of feeding bouts observed (n)	Total sec observed for feeding rate	Total no. of probes in determination of feeding rate	$\bar{x}$ feeding rate (probes/sec)
<i>Selasphorus calliope</i>				
Adult male	14	374.5	294	0.78
Female and immature	13	550.8	402	0.73
Total	27	925.3	696	0.75
<i>S. rufus</i>				
Adult male	61	1,751.5	929	0.53
Female and immature	15	379	202	0.53
Total	76	2,130.5	1,131	0.53

Generally, Rufous Hummingbirds on Wheeler Peak were strongly territorial while Calliope Hummingbirds were not. Territoriality was not quantified, but adult male Rufous were seldom seen apart from a defended territory. Adult male Calliope were seen to establish territories twice, both being defended for less than 1 day.

The Calliope's feeding strategy appeared to be one of robbing Rufous territories. I did not determine whether they followed regular routes, using a traplining strategy (Feinsinger and Chaplin 1975), but they were chiefly nonterritorial foragers. When feeding within Rufous territories, Calliope exhibited behaviors they were not seen to engage in elsewhere such as exceptionally low flight and perching on the ground.

The feeding rate, measured in probes per second, of *S. calliope* was found to be 0.75, significantly faster than the 0.53 probes per second recorded for *S. rufus* ( $t = 7.52$ ,  $df = 101$ ,  $P < 0.001$ ) (Table 1). Feeding rates of males did not differ significantly from those of females for either species.

The feeding height distribution of each species differed significantly from random (Rufous:  $\chi^2 = 320.09$ ,  $df = 4$ ,  $P < 0.001$ ; Calliope:  $\chi^2 = 238.45$ ,  $df = 4$ ,  $P < 0.001$ ) and from each other ( $\chi^2 = 486.27$ ,  $df = 4$ ,  $P < 0.001$ ). The Calliope fed primarily on lower flowers than did Rufous, making more probes in the 10–20 cm category (35.9%) than in any other, while the Rufous made the largest proportion of their probes (30.3%) in the 30–40 cm category.

The feeding height of females and immatures of both species differed significantly from that of adult males and from females and immatures of the other species ( $P < 0.001$ ). Females and immature hummingbirds concentrated their feeding activity in the central (20–30 cm) category. Female and immature Calliope showed a tendency to select low flowers, and female and immature Rufous showed a tendency to select high flowers, but neither Rufous nor Calliope females and immatures deviated from the central height category to the extent that adult males did (Table 2).

#### DISCUSSION

Initially it would appear that the Calliope's lower feeding height and faster rate are elements of a raiding strategy by which they feed inconspicuously within a Rufous territory in order to get as much nectar as possible before being chased away. A faster feeding rate would have reduced the time that Calliope were visible to Rufous and thus vulnerable to aggression. But there are several other possible explanations for this discrepancy in feeding rates.

For one, Calliope may have probed faster to compensate for a lower nectar yield per probe. When feeding within the territory of a Rufous the Calliope would not know which flowers had recently been fed upon and may have made a significant number of dry probes. Yeaton and Laughrin (1976) mention this possibility with reference to Anna's Hummingbirds (*Calypte anna*) feeding within territories of Allen's Hummingbirds

TABLE 2. Percentages of feeding probes made in different height categories by Calliope and Rufous hummingbirds at Wheeler Peak, White Pine County, Nevada.

	No. of feeding probes	Feeding height categories (%)				
		0–10 cm	10–20 cm	20–30 cm	30–40 cm	40–50 cm
<i>Selasphorus calliope</i>						
Adult male	180	27.2	45.5	21.1	6.1	0
Female and immature	399	18.3	31.6	34.8	15.3	0
Total	579	21.1	35.9	30.5	12.4	0
<i>S. rufus</i>						
Adult male	717	0.5	10.7	23.4	34.3	31.0
Female and immature	158	2.5	8.9	55.0	12.0	21.5
Total	875	0.9	10.4	29.1	30.3	29.3

(*Selasphorus sasin*). However, due to the separation in feeding heights of the Wheeler Peak hummingbirds the two species were feeding primarily on different flowers, so the influence of Rufous competition on Calliope nectar-gathering efficiency was probably less than it would have been had they fed on the same flowers.

Another possibility is that lower *Castilleja* flowers may have produced less nectar than the higher flowers. If so the Calliopes would have to feed either faster or for longer periods of time in order to obtain sufficient quantities of nectar.

Finally, the Calliopes may have fed faster due to their higher metabolic rate. Hainsworth and Wolf (1972) found that small hummingbirds have less storage capacity in their crops relative to their gram specific metabolic rates than large hummingbirds. One would expect a large discrepancy between Rufous and Calliope hummingbirds with respect to crop capacity/metabolic rate/gram because as body weight decreases, crop volume decreases linearly while metabolic rate increases exponentially, and Rufous Hummingbirds weigh 24.4% more than Calliopes (Johnsgard 1983).

There are also a number of possible reasons for the Calliope's lower feeding height. For one, the Calliopes may be responding to Rufous' feeding height preference rather than aggression. The Rufous were also selective with respect to the height of the flowers on which they fed, making 88.4% of their feeding probes in flowers higher than 20 cm. It is possible that Calliopes extracted more nectar per probe by selecting flowers that Rufous neglected than they would have had they fed randomly with respect to height.

The discrepancy in feeding strategy between two species may be a response by one species to the presence of the other (MacArthur 1958). Proof requires an experiment in which the behavior of one species is observed in the presence and absence of the other. I did not perform such an experiment, but I would speculate that in this case the Calliope Hummingbirds were responding to interspecific territoriality by Rufous Hummingbirds by employing the aforementioned raiding strategy. Several field observations support this.

For one, Calliopes exhibited two behaviors only within Rufous territories that would have reduced their visibility to the defending Rufous Hummingbirds. First, when perching within a Rufous territory the Calliopes chose low perches, within 0.25 m of the ground, as opposed to perches 1 to 2 m high when defending territories of their own. Four times I saw Calliopes perch low within Rufous territories and remain unmolested for more than 5 min. They were chased away only when they began feeding. Twice I saw Calliopes perch on the ground within Rufous territories. Exceptionally low flight was also observed on two occasions: once when an adult male Calliope made a slow flight of about 1.5 m, never rising more than 0.05 m from the ground. He went around rather than over the rocks and vegetation in his path. On the other occasion an adult male Calliope flew rapidly into a Rufous territory, flying about 15 m in a straight line approximately 0.1 m from the ground, then perched on a stick about 1 cm high. Neither of these birds was chased by the resident Rufous until they began feeding. These behaviors were so distinctly different from normal hummingbird behavior that it appeared as though the Calliopes were

actively trying to avoid detection by the Rufous Hummingbirds that defended the territories.

Lyon (1976) observed another small species, the White-eared Hummingbird (*Hylacharis leucotis*), exhibiting similar behavior. Noting that White-ears fed on lower flowers within the territories of the larger Blue-throated Hummingbirds (*Lampornis clemenciae*) than without, he hypothesized that their lower feeding height was a learned response to Blue-throat aggression.

The feeding height preference of female and immature hummingbirds complicates the problem. I know of no satisfactory explanation for the difference between feeding heights of males and females.

In comparing my observations with those of others, it would appear that Calliope Hummingbirds are variable with respect to foraging strategy. The Calliopes that I observed and those reported by Armitage (1955) employed a feeding strategy of raiding the territories of Rufous Hummingbirds, whereas those observed by Bailey and Niedrach (1965), Cody (1968), and Austin (1970) defended territories against a total of five species of larger hummingbirds. It is interesting to note that the Calliopes Bailey and Niedrach saw fed on lower flowers than did the other species in the vicinity. This may indicate that the Calliopes' feeding height is not necessarily a response to Rufous aggression.

In summary, Rufous and Calliope hummingbirds were observed on Wheeler Peak, White Pine County, Nevada, where they fed almost entirely on *Castilleja miniata*. Rufous were highly territorial, while Calliopes fed by raiding Rufous territories. Measurements of feeding rates and heights revealed that Calliope Hummingbirds fed significantly lower and faster than did Rufous Hummingbirds. It is possible that the Calliopes' low and fast feeding behavior enhanced the effectiveness of this raiding strategy.

I would like to thank Richard E. Johnson for his invaluable assistance in the preparation of this manuscript, and Anne Evett for her support in the field.

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*The Condor* 90:236-239  
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## NESTING OF THE WING-BANDED ANTBIRD AND THE THRUSH-LIKE ANTPITTA IN FRENCH GUIANA<sup>1</sup>

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**Key words:** *Myrmornis torquata*; *Myrmothera campanisona*; *Formicariidae*; *Thamnophilidae*; *French Guiana*; nest; eggs.

Typical ground-dwelling antbirds are among the least-known formicariids of the neotropical rain forests. They are usually neither shy nor very rare, but their secretive behavior forces the field ornithologist to rely mainly on vocalizations to detect them. In French Guiana the Thrush-like Antpitta (*Myrmothera campanisona*) and the Wing-banded Antbird (*Myrmornis torquata*) are widespread in damp, dark understories (often in old treefall gaps) and in the hilly, humid understory of the inland mature forest respectively (Thiollay 1986, pers. observ.). Their nests have not been described to date.

### WING-BANDED ANTBIRD

On 27 July 1985, Dujardin found a nest of the Wing-banded Antbird in the upper drainage of the Litany River along the Surinam border, 2 km from the mouth of the Koulé-Koulé (2°26'N, 54°28'W), at an elevation of 155 m. The nest site was at the bottom of a small hill in tall rain forest (canopy at 40 to 60 m) about 100 m from the river. The nest was hanging 2 m above ground from a lateral fork 10 cm from the trunk of a sapling 3.5 m high. The shallow cup, 5 cm high, 3 cm deep, with an internal diameter of 6 to 7 cm, was made of twigs and rootlets (Fig. 1). The clutch consisted of a single egg (26.2 × 18.6 mm). It was creamy white with abundant violet-brown streaks and spots (Fig. 2). The markings were more distinct and darker at the larger end. The female was incubating the egg on 28

July 1985, but lack of time did not permit us to conduct further observations. Later observations of nine different families confirmed that the male is involved in rearing the young. The families were encountered on 20 March 1986 (one family), from 2 to 17 October 1986 (six families), and from 30 April to the end of May 1987 (two families), in the middle Arataye River drainage, around the newly established Biological Station of the Montagne des Nouragues (4°05'N, 52°43'W) (see de Granville [1982] and Atlas de la Guyane [1979] for topographic and climatic descriptions of the sites mentioned in this paper).

Wing-banded Antbirds foraged on slopes with abundant vines and low bushes, by hopping along the ground and vigorously searching with the bill in the litter. Thick, dead leaf accumulations seem to be preferred since birds spend more time foraging in such places than in areas with a thin litter. Foot-scratching has never been observed, and Wing-banded Antbirds always use their straight, long bill in a very fast motion in order to turn or throw dead leaves. Leaves are never seized by the bill. The foraging Wing-banded Antbird may even totally disappear for a few seconds under the largest leaves.

All families we observed consisted of a pair with a single young. Until the time we got the chance to catch a flightless fledgling, the young antbirds seemed to wear a plumage very close to that of the adult, neither male (with a black throat) or female (with a rufous throat). In fact, a transitional plumage has been assessed in a fledgling examined closely and regularly throughout 1 month. On 22 May 1987, we located a *M. torquata* family in a well-known and daily-searched sector where no bird was seen previously. Both parents were easily alarmed, a behavior much less sustained with old fledglings. On 23 May we got the opportunity to catch and ring the flightless fledgling. All the head, nape, throat, and the underparts (contour feathers) were covered by

<sup>1</sup> Received 19 November 1986. Final acceptance 2 October 1987.