

POST-BREEDING TERRITORIALITY AND FORAGING BEHAVIOR  
IN COSTA'S HUMMINGBIRD (*CALYPTE COSTAE*)

MICHAEL L. AVERY AND CHARLES VAN RIPER III

*National Park Service, Cooperative National Park Resources Studies Unit,  
Wickson Hall, University of California, Davis, CA 95616*

*Present address of M.L.A.: United States Department of Agriculture,  
Denver Wildlife Research Center, Florida Field Station,  
2820 E. University Avenue, Gainesville, FL 32601*

*Present address of C.V.R.: National Park Service,  
Cooperative National Park Resources Studies Unit,  
Northern Arizona University, Box 5613, Flagstaff, AZ 86011*

Costa's hummingbird (*Calypte costae*) is a xerophilic species that breeds in desert areas of southern California, Arizona, and adjacent Mexico from late February into early spring (Johnsgard, 1983). As desert flower availability declines, many individuals migrate northward into coastal chaparral areas (Stiles, 1972; Weathers, 1983), a period during which very little is known about Costa's hummingbird. Some birds possibly breed a second time in the chaparral of the Coast Range, but this remains to be verified (Stiles, 1972).

Here, we document foraging and territorial behavior of Costa's hummingbirds temporarily resident at Pinnacles National Monument in central California on the northern edge of the species' breeding range (American Ornithologists' Union, 1983; Baltosser, 1989). Prior to 1984, only one sighting had occurred at Pinnacles (Avery and van Riper, 1986), but several sightings were made in spring of 1984 and 1985 at which time males were observed engaged in elliptical dive-and-whistle display flights. The recent sightings coincide with an apparent northward range extension of Costa's hummingbirds in California (LeValley and Campbell, 1984; Baltosser, 1989).

Pinnacles National Monument is located in Monterey and San Benito counties, approximately 65 km inland, and situated at the southern end of the Gabilan Mountains, part of the Coast Range of central California. The study site was an open area on the east side of the Monument adjacent to Chalone Creek at a dense stand of *Trichostema lanatum* (Labiatae), a woody shrub with pale blue to purple flowers adapted for hum-

mingbird pollination (Spira, 1980). Other vegetation included several large live oaks (*Quercus agrifolia*) and scattered patches of chamise (*Adenostema fasciculatum*), redberry (*Rhamnus crocea*), and elderberry (*Sambucus* sp.) shrubs. Annual grasses and yellow star thistle (*Centaurea solstitialis*) dominated the ground cover.

In both 1985 and 1986, we visited the study site on nine days between 23 April and 27 June, and spent approximately 80 hours each year mist-netting birds and observing behavior. A 60- × 30-m area was gridded into 10- × 10-m squares. On a scale drawing of that area, we plotted perch sites used by territorial birds and locations of altercations between territory holders and intruders to estimate size and extent of defended areas. We also plotted locations of *T. lanatum* plants and we used area covered by those shrubs as an estimate of territory quality.

At irregular intervals throughout the day, we recorded total time spent foraging, defending territories, and perching by territorial individuals kept continuously in view for up to 30 min or until lost from sight. To aid in identifying individuals, we glued small pieces of colored plastic flagging to the back feathers of some mistnetted birds. We identified unmarked territorial birds by distinctive plumage features. Species and age/sex determinations were made with the aid of standard references (Stiles, 1971; Johnsgard, 1983). Birds having broad, pale feather edgings were designated as juveniles. Juvenile males were distinguished from juvenile females by possession of substantial numbers of purple gorget feathers;

TABLE 1—Age and sex of Costa's hummingbirds mistnetted at Pinnacles National Monument in May and June, 1985–1986.

Year	Adults		Juveniles		Unknown
	Male	Female	Male	Female	
1985	4	3	8	4	5
1986	6	3	6	2	8
Totals	10	6	14	6	13

however, sex of juvenile birds could not be determined in all cases.

We estimated seasonal and daily nectar availability by extracting nectar from flowers with 20- $\mu$ l capillary tubes. We measured sugar with a temperature compensated hand-held refractometer and converted these measurements to sucrose-equivalent sugar concentrations (Bolten et al., 1979). We estimated hourly nectar production by measuring nectar in open flowers and in nearby flowers from which birds and insects had been excluded for 3–5 hours (e.g., Carpenter, 1983). Mean nectar volume in open flowers at the start of the measurement period was subtracted from mean nectar volume in protected flowers at the end of the interval and the difference was divided by the length of the measurement interval.

During May–June 1985 and 1986, 49 Costa's (Table 1), 12 black-chinned (*Archilocus alexandri*), 9 Anna's (*Calypte anna*), and 2 Allen's (*Selasphorus sasin*) hummingbirds were captured. Except for Costa's, each species is known to nest within the Monument (Avery and van Riper, 1986). Costa's hummingbirds occurred on the study site from 22 May to 27 June 1985 and from 23 May to 23 June 1986.

On 23 May 1986, we netted and marked a male Anna's hummingbird that perched atop an oak snag adjacent to the study site and displayed over the entire study site. Several times it chased other birds, including a nonterritorial male Costa's, from flowering shrubs. On 1 June, the marked Anna's was singing and defending only the north edge of the study site. One Costa's hummingbird was atop the oak snag and 3 others had territories among the shrubs. By 13 June, there were 7 territorial male Costa's and no Anna's.

In 1986, territorial Costa's hummingbirds spent 62.6% to 92.8% of their time perched within their territories (Table 2). Overall, adults spent more time chasing intruders and less time foraging than

TABLE 2—Activity budgets of territorial Costa's hummingbirds and area within territories covered by *Trichostema lanatum* bushes during June 1986 at Pinnacles National Monument, Paicines, CA. Adult birds are indicated by the prefix A, and juveniles by the prefix J.

Bird	Area of <i>T. lanatum</i> (m <sup>2</sup> )	Total time observed (min)	Activity (% of total time)			
			Perch	Feeding on		
				Nectar	Insects	Chase
A1	7.0	40.3	92.8	6.5	0	0.7
A2	13.5	51.3	62.6	24.2	2.3	10.9
A3	10.8	13.5	72.6	12.5	0.2	13.4
J1	3.8	81.0	80.4	15.4	0.3	3.9
J2	2.8	25.5	82.2	17.2	0	0.6
J3	2.3	37.6	67.9	27.2	0	4.9

did juvenile birds. Hawking for insects constituted a small portion of most birds' time budget, but some sallies after small insects lasted several seconds ( $\bar{X} = 3.6$  s,  $SE = 0.5$ ,  $n = 25$ ).

Territories of 3 adult males averaged 10.4 m<sup>2</sup> ( $SE = 1.9$ ) of coverage by *T. lanatum* bushes compared to 3.0 m<sup>2</sup> ( $SE = 0.4$ ) for the juvenile birds ( $P = 0.018$ ;  $F = 14.87$ ; 1, 5 *d.f.*). The area covered by *T. lanatum* was correlated ( $r = 0.77$ ;  $t = 2.39$ ;  $0.10 > P > 0.05$ ) with the percentage of time spent chasing intruders (Table 2). We observed no territorial female Costa's hummingbirds.

Our results suggest that adult male Costa's left the area before juveniles, possibly in response to declining flower abundance. For both years combined, 7 of the 12 male Costa's captured before 10 June were adults compared to 3 of 12 after 10 June ( $P < 0.10$ ;  $\chi^2 = 2.74$ ; 1 *d.f.*).

During May 1986, the mean amount of nectar available in *T. lanatum* flowers throughout the day ranged from 1.8 to 3.0  $\mu$ l/flower (Table 3). Sugar content ranged as high as 0.83 mg/flower, but on some dates we could not collect enough nectar to measure concentrations. The standing nectar crop declined in 1985 after 13 June, but we did not detect such a response in 1986 when nectar availability appeared to be greater (Table 3).

*Trichostema lanatum* flowers began to open in the first week of May and peaked in abundance 3–4 weeks later. We estimated flowers to be approximately 90% gone by the last week of June.

TABLE 3—Nectar availability, sucrose equivalent sugar content, and nectar production in *Trichostema lanatum* flowers at Pinnacles National Monument.

Date	Time	n	Nectar ( $\mu\text{l}/\text{flower}$ )		Sugar content (mg/flower)	
			$\bar{X}$	SE	$\bar{X}$	SE
22 May 1985	1400	18	0.3	0.1	0.09	0.01
13 Jun 1985	0830	20	1.7	0.2	0.39	0.02
18 Jun 1985	1730	20	0.1	0.1	unmeasurable	
19 Jun 1985	0900	18	0.1	0.1	unmeasurable	
23 May 1986	1000	20	2.3	0.3	0.54	0.02
23 May 1986	1300	20	3.0	0.5	0.72	0.02
24 May 1986	0700	20	2.7	0.4	0.63	0.01
14 Jun 1986	1900	18	1.8	0.4	0.46	0.03
15 Jun 1986	0730	15	3.5	0.4	0.83	0.02

  

Date	Interval	n	Final nectar content ( $\mu\text{l}$ )		Nectar production ( $\mu\text{l}/\text{h}$ )
			$\bar{X}$	SE	
13 Jun 1985	0830–1130	15	3.0	0.2	0.43
19 Jun 1985	0900–1200	20	1.7	0.2	0.48
23 May 1986	1000–1500	20	5.3	0.4	0.60
23 May 1986	1300–1600	20	5.9	0.3	0.97

Flowers that were bagged for 3–5 h accumulated as much as 5.9  $\mu\text{l}$  of nectar (Table 3). Rates of nectar production varied from 0.43 to 0.97  $\mu\text{l}/\text{flower}/\text{h}$ . Previously published information indicates nectar volume of 5.4  $\mu\text{l}/\text{flower}$  (Spira, 1980), and Stiles (1972) included *T. lanatum* in a group of species with daily nectar production of 10–25  $\mu\text{l}/\text{flower}/\text{day}$ .

Although males were observed displaying at Pinnacles from late March through April (Avery and van Riper, 1986), nesting was unrecorded, and additional study of Costa's hummingbird at Pinnacles is warranted to clarify breeding status there. We suspect that the birds observed during May–June were post-breeding transients from southwestern California deserts that were present at Pinnacles only long enough to exploit the flowering of *Trichostema lanatum*. Stiles (1972) found that Costa's hummingbirds arrived in the Santa Monica Mountains, approximately 320 km south of Pinnacles, during March–April and the peak of the breeding season was in May. There, birds remained in chaparral throughout summer until departing for Mexican wintering grounds in September. As at Pinnacles, *Trichostema lanatum* was the major food plant in the dry interior chaparral during early summer.

Territoriality in the nonbreeding season is common among hummingbirds (Stiles, 1972).

Costa's hummingbirds at Pinnacles in May and June were highly territorial and appeared dominant over the other hummingbird species. We observed one resident Anna's that attempted to control patches of *Trichostema lanatum* but was supplanted by Costa's. Neither black-chinned nor Allen's established territories, although they occasionally intruded. Our findings are thus at variance with Stiles (1972) who reported that in the Santa Monica Mountains, Anna's were dominant over black-chinned hummingbirds, which in turn were dominant over Costa's at feeding sites. Also, Hixon and Carpenter (1988) found that Costa's were subordinate to the rufous hummingbirds (*Selasphorus rufus*) near Bishop, California in the Sierra Nevada. The apparent success of the Costa's hummingbirds defending feeding territories at Pinnacles might be due to their numerical superiority or to habitat characteristics that made territoriality unprofitable for the other species.

In several respects, the territorial behavior of nonbreeding Costa's resembles closely that of Anna's: (1) adult and subadult males defend feeding territories; (2) subadult males hold smaller territories with fewer flowers than do adult males; (3) as flower abundance declines, adult males abandon territories more quickly than do subadults; and (4) females do not hold feeding territories. Further similarities in the ecology of these

closely related species may emerge as more becomes known of the biology of Costa's hummingbird.

The staff of the Pinnacles National Monument were extremely supportive during the study. In particular, we thank R. Broyles, E. Carlson, and S. de Benedetti for their help and encouragement. This research was partially supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History.

#### LITERATURE CITED

- AMERICAN ORNITHOLOGISTS' UNION. 1983. Checklist of North American birds. Sixth ed. Amer. Ornithol. Union, Washington, D.C.
- AVERY, M. L., AND C. VAN RIPER III. 1986. Bird community survey at Pinnacles National Monument. U.S. Natl. Park Serv., Coop. Natl. Park Resource. Stud. Unit Tech. Rep. 24, Davis, California, 83 pp.
- BALTOSSER, W. H. 1989. Costa's hummingbird: its distribution and status. *West. Birds*, 20:41-62.
- BOLTEN, A. B., P. FEINSINGER, H. G. BAKER, AND I. BAKER. 1979. On the calculation of sugar concentration in flower nectar. *Oecologia*, 41:301-304.
- CARPENTER, F. L. 1983. Pollination energetics in avian communities: simple concepts and complex realities. Pp. 215-234, in *Handbook of experimental pollination ecology* (C. E. Jones and R. J. Riddle, eds.). Van Nostrand Reinhold Co., New York.
- HIXON, M. A., AND F. L. CARPENTER. 1988. Distinguishing energy maximizers from time minimizers: a comparative study of two hummingbird species. *Amer. Zool.*, 28:913-925.
- JOHNSGARD, P. A. 1983. *The hummingbirds of North America*. Smithsonian Institution Press, Washington, D.C.
- LEVALLEY, R., AND K. F. CAMPBELL. 1984. The spring migration: March 1-May 31, 1984, middle Pacific Coast region. *Amer. Birds*, 38:952-957.
- SPIRA, T. P. 1980. Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). *Amer. J. Bot.*, 67:278-284.
- STILES, F. G. 1971. On the field identification of California hummingbirds. *Calif. Birds*, 2:41-54.
- . 1972. Food supply and the annual cycle of the Anna hummingbird. *Univ. Calif. Publ. Zool.*, 97:1-109.
- WEATHERS, W. W. 1983. *Birds of southern California's Deep Canyon*. University of California Press, Berkeley, California.