FALL RESOURCE DIVISION IN SANTA CRUZ ISLAND HUMMINGBIRDS

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Six species of hummingbird breed in mainland California, but only the Anna's Hummingbird (*Calypte anna*) remains year-round in the vicinity of its breeding habitat. However, on some of the Channel Islands, particularly Santa Cruz and Santa Catalina, and on the island-like Palos Verdes Peninsula, Anna's and the insular race of the Allen's Hummingbird (*Selasphorus sasin sedentarius*) are both resident year-round. Temperate zone hummingbirds, when not separated by habitat differences, generally defend territories between, as well as within, species (Pitelka 1951, Legg and Pitelka 1956, Cody 1968), presumably the result of their specialized and relatively similar feeding behavior. Grant (1966) has suggested that ecologically similar species do not generally occur together in insular situations. On the large, habitat-diverse islands of the West Indies, Lack (1971) reported that hummingbirds were separated most frequently by habitat. Whenever Lack found 2 species of hummingbirds using the same habitat, they were different in body size (as measured by wing and/or culmen length), indicating to him that the species were occupying different ecological niches. For example, the larger member of a sympatric pair of hummingbirds had on the average 1.55 times longer wings and 2.08 times longer culmen than the smaller member (Lack 1971: 230). It is therefore interesting that 2 relatively similarly-sized species of hummingbird (Anna's Hummingbird has 1.22 times longer wings and 1.05 times smaller culmen than the resident race of Allen's Hummingbird) should be resident year-round on the Channel Islands.

This paper examines the resource use of Anna and Allen hummingbirds on Santa Cruz Island, to determine how these species coexist between September and early November. This period is deemed critical for the continued existence of the 2 hummingbirds because only 2 native plants, California fuchsia species *Zauschneria californica* and *Z. cana*, are flowering on the island. These food plants are not abundant and are found only infrequently in dense concentrations, so both species of hummingbirds aggregate in the bottoms of canyons and washes to feed on *Zauschneria* nectar. Also during this period of the year on Santa Cruz Island, insect availability reaches its lowest level (Yeaton 1972), presumably due to the previous 3 months in which there is no rain. During the remainder of the year the hummingbirds are separated by habitat on Santa Cruz Island. Allen's are found in the denser and taller chaparral of the north-facing slopes and in riparian woodlands,

while Anna's occupy more open chaparral of south-facing slopes, pine forests, and oak woodlands (Yeaton, pers. obs.). During this time, from December through August, on Santa Cruz Island many food plants and insects are available for hummingbirds.

STUDY AREAS AND METHODS

Santa Cruz Island (N 34° W 119°), a member of the northern Channel Islands group, is 30 km offshore from Santa Barbara, California. It is 250 km^2 in area and contains many habitat types of which grassland, chaparral, and pine forest are most abundant. The avifauna of Santa Cruz Island, as well as the other Channel Islands, is well known (Johnson 1972, Yeaton 1972).

We studied hummingbirds at 3 sites containing *Zauschneria* spp. during October, 1972. A chaparral situation with a varying degree of canopy cover on north- and south-facing slopes was observed in Canada d'Islay which opens into the central valley of the island. North-facing slopes were densely vegetated while south-facing slopes were grassy with scattered shrubs. In addition to *Zauschneria*, *Eucalyptus* was present near the mouth of the canyon. Along the moist canyon floor of an unnamed tributary of Water Canyon on the north side of the island, a second site composed of the vegetation type coastal sage, intermingled with some chaparral elements, was observed. Surrounding the general area of this site were grasslands and scattered oaks. The third site observed consisted of a chaparral-oak woodland transition type of vegetation in Canada de las Sauces de l'Oeste in the southwestern part of the island.

Birds at the 3 sites were censused by walking slowly in the bottoms of the canyons, recording the species of the individuals holding feeding territories, and mapping the extent of these feeding territories. We define feeding territory as being 2 or more flowering clumps of *Zauschneria* spp. defended by an individual against other hummingbirds. The shape and size of feeding territories varied with the topography of the canyon sides. Most territories were elongate, centered in the bottom of the canyon and extending up the sides of the canyon. Hummingbirds holding adjacent feeding territories in the bottom of each canyon were studied, and the number and distribution of flower clumps within an individual's feeding territory were determined. In addition, for each territory the distance between the flower clumps farthest apart was measured. This distance represents the maximum distance within the territory which a hummingbird had to fly to feed.

In Canada d'Islay and Water Canyon the sizes of flower clumps were compared. Since each flower clump was roughly spherical in shape, average diameter gave us a relative measure of clump size. Flowers are distributed over the surface of the clumps. Assuming that a constant proportion of flowers on each bush is producing nectar suitable for hummingbird use, larger bushes have more flowers producing nectar than smaller bushes.

We observed the behavior of 2 Anna's Hummingbirds in Canada d'Islay for a total of 9.75 activity hours and 3 Allen's Hummingbirds in Water Canyon for a total of 7.75 activity hours. We quantified the flower clump use of each species by mapping the location of bushes within an individual's feeding territory and then noting the feeding pattern of that individual on these flower clumps. Also we recorded the length of the feeding bouts and the time between bouts for a territorial individual, and the use of a territorial individual's flower clumps by other hummingbirds. These feeding observations were made between 31 October and 3 November 1972 from 09:00 to 13:00 under sunny and cloudless weather conditions.

Histograms showing the pattern of occurrence and duration of feeding bouts were

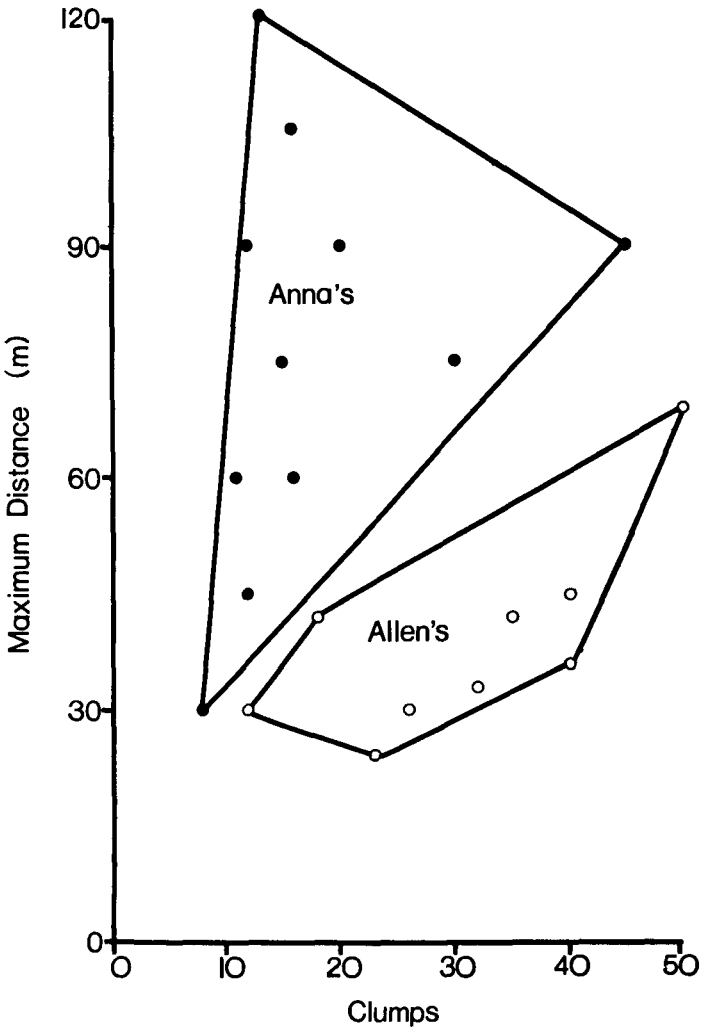

FIG. 1. Comparison of feeding territories of Allen and Anna hummingbirds with reference to number of *Zauschneria* clumps and maximum distance between defended clumps.

drawn. The average duration of a feeding bout (defined as a period of feeding by an individual separated by at least 5 min from the next onset of feeding) and the average time between bouts were then obtained from these histograms. When an individual had not fed on flower clumps for 60 min, we ceased observations and the time between feeding bouts was considered to be 60 min. The mean duration of a feeding bout was obtained by dividing the total number of seconds spent feeding by the number of feeding bouts.

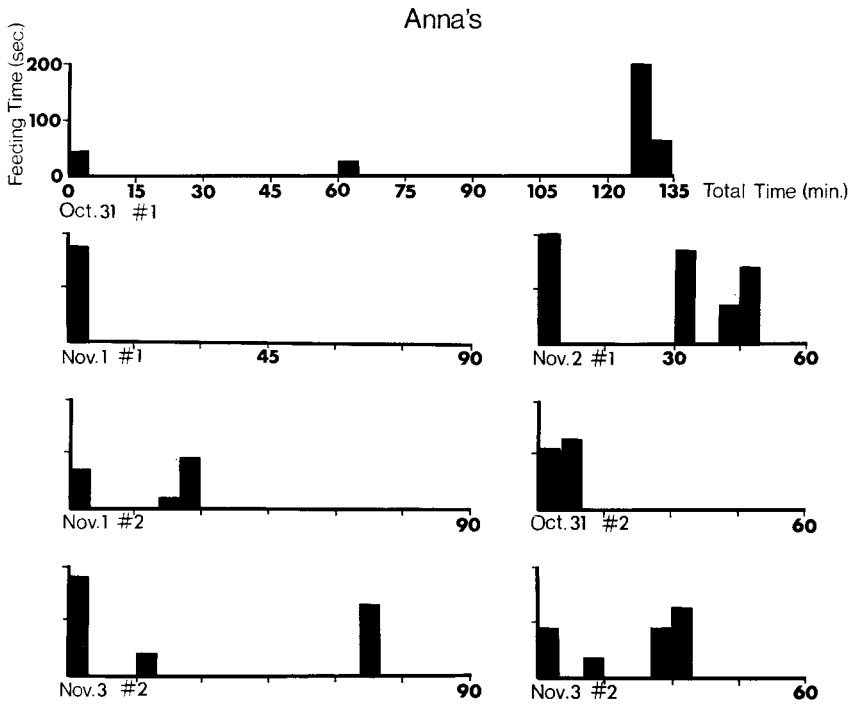

FIG. 2. Anna Hummingbird feeding bouts on Santa Cruz Island between 09:00 and 13:00; # represents bird watched. The horizontal axis represents the total time in min spent watching an Anna Hummingbird, starting with the first feeding bout observed and continuing until observations on that individual ceased.

RESULTS

In Canada d'Islay there were 7 Anna feeding territories, in Sauces 4 Anna feeding territories and 1 Allen, and in Water Canyon 3 Anna and 15 Allen feeding territories. The major differences in the feeding territories of the 2 species seemed to be the abundance of and maximum distance between *Zauschneria* plants (Fig. 1). Allen Hummingbirds had smaller feeding territories containing a high density of clumps of *Zauschneria*. The feeding territories of Anna Hummingbirds were larger and contained fewer food plants.

Analysis of the feeding behavior of the 2 species indicated differences in the method of harvesting nectar from the flowers (Figs. 2 and 3). Allen Hummingbirds fed more frequently and for shorter periods of time than did Annas. Allens fed every 16.9 min (S.E. = 3.5 min) on the average for

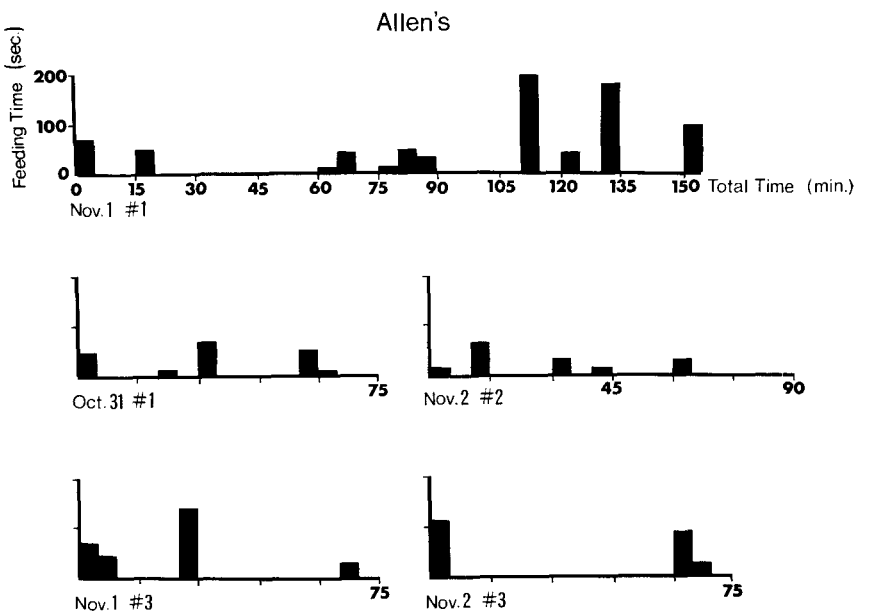

FIG. 3. Allen Hummingbird feeding bouts on Santa Cruz Island between 09:00 and 13:00; # represents bird watched. The horizontal axis represents the total time in min spent watching an Allen Hummingbird, starting with the first feeding bout observed and continuing until observations on that individual ceased.

a mean duration of 1.7 min (S.E. = 0.2 min) whereas Annas averaged 31.8 min (S.E. = 7.3 min) between bouts which lasted an average of 2.8 min (S.E. = 0.3 min). The average distance flown during a feeding bout was 16.4 m ($S_{\bar{x}}$ = 6.3 m) for Allens and 31.1 m ($S_{\bar{x}}$ = 8.2 m) for Annas. Although Allen Hummingbirds visited only 3.1 flower clumps per bout (S.E. = 0.4) while Annas visited 4.2 flower clumps (S.E. = 0.5), when corrected for the size differences of flower clumps in Allens (mean = 105.6 cm, S.E. = 14.6 cm diameter) and Annas (mean = 77.6 cm, S.E. = 10.5 cm diameter) feeding territories, the number of flowers visited during a feeding bout by Allens was potentially greater assuming at least equal numbers of nectar producing flowers per average size flower clump in each species' feeding territory.

Our observations also indicated that within an individual Allen feeding territory, 38% of the flower clump feeding time was used by an individual other than the territory owner. The comparable figure for Anna Hummingbirds was 8%.

DISCUSSION

The distribution patterns of Allen and Anna hummingbirds during the fall in the 3 canyons seemed to be affected by the abundance and spacing of *Zauschneria.* Canada d'Islay contained only Annas whereas both species were found in Sauces and Water canyons. We have shown that the hummingbirds divide the *Zauschneria* resource on the basis of its density. In Canada d'Islay where only Annas were found, *Zauschneria* plants were sparsely distributed. In Sauces and Water canyons a similar sparse distribution existed and Annas were present. But in addition many portions of these latter canyons had a large number of *Zauschneria* plants located close together, due in part to the presence of permanent streams. In these latter areas Allen Hummingbirds established their feeding territories.

What are the differences between the species that enable or require one to use a concentrated and the other a sparse resource? Intuitively the best kind of feeding territory would seem to be one in which food plants are abundant and close together, minimizing the energy expenditure for maintenance and defense of the territory. Alternatively a dense nectar source might also be attractive to many other individuals and lead to increased energy costs for defense of a feeding territory (Gill and Wolf 1975). Allen Hummingbirds crowded into areas with high densities of *Zauschneria* clumps. While these areas might be favorable in terms of nectar availability they are also areas which are attractive to other individuals. The 38% of time (as opposed to 8% for Annas) in which individuals other than the territory holder used the feeding territory in areas of high *Zauschneria* availability may be indicative of the extra pressure placed on these high density areas. Why then were Allens only found in such areas? Allen Hummingbirds weigh about 1.18 times less than Annas (Stiles 1974). Smaller hummingbirds have less storage capacity in their crops relative to their metabolic rates per gram than do larger hummingbirds (Hainsworth and Wolf 1972). A smaller crop means less nectar can be gathered and stored per feeding flight and hence for an Allen Hummingbird to maintain itself, it must feed at shorter intervals than do the larger Anna Hummingbirds. Allen Hummingbirds fed twice as often as did Annas. In conjunction with the increased rate of feeding in Allen Hummingbirds is the problem of nectar renewal in the *Zauschneria* plants. Shorter return times to a given plant meant that there was less time for nectar levels to renew themselves and so Allen Hummingbirds by feeding more frequently actually may have harvested less nectar per flower visit. In addition individuals attempting to steal nectar were likely doing it at a reduced efficiency since they were not familiar with which *Zauschneria* bushes had been harvested last by the territory holder. As a result of the combination of small crop size, necessitating shorter intervals between feed-

ing bouts, and the relatively slow renewal rates of the flowers, Allen Hummingbirds were obligated to establish feeding territories in areas of dense *Zauschneria* concentrations in order to optimize energy expenditures.

Anna Hummingbirds, by waiting longer, allow the nectar more time to renew and increase the amount of nectar harvested per feeding flight. Longer waiting times alone would allow Annas to use a feeding territory containing a sparser resource. Contributing also to use of a sparser resource is a possible reduction in defense costs due to the reduced attractiveness of areas with lower densities of food plants. Of course defense costs are compromised somewhat by the necessity to protect the few but rich nectar sources available to a territorial individual from the possible raid of a neighboring individual. The choice of perches by Anna Hummingbirds which allowed observation of all of an individual's food plants and the relatively low percentage of time spent feeding on the food plants lost to intruders (8%) would seem to indicate a more effective territorial defense by Annas of their sparse food plants than by Allens in their density *Zauschneria* feeding territory.

We did not observe the mechanism by which the slightly smaller Allen Hummingbirds excluded Annas from the high density *Zauschneria* areas. Stiles (1973) recorded the displacement of Anna Hummingbirds at a rich nectar source on the mainland by the smaller, migratory Allen Hummingbird (*Selasphorus s. sasin*). In that study the great number of migrants produced a "swamping" effect, forcing Annas to spend such a large proportion of time in defense of food bushes that Annas abandoned the area. A similar mechanism might be invoked for territory establishment by Allen Hummingbirds on Santa Cruz Island.

Why Allen Hummingbirds are not resident on the adjacent mainland (other than on the insular Palos Verdes Peninsular) is unknown. Our preliminary observations from the Santa Monica Mountains indicate that *Zauschneria* is sparsely distributed and does not attain the compact distribution necessary for establishment of feeding territories by Allens. The mainland distribution of *Zauschneria* may be the result of fire disturbance which is relatively common on the mainland compared with the island. An additional factor preventing Allens from being a resident species on the mainland may be increased competition from other hummingbird species migrating south in the fall. Few, if any, hummingbirds have been recorded in migration on the Channel Islands (Grinnell and Miller 1944).

SUMMARY

The sympatry of 2 hummingbird species, Anna's (*Calypte anna*) and Allen's (*Selasphorus sasin sedentarius*), on Santa Cruz Island, California, was examined during the fall when there is only one abundant food resource, *Zauschneria* sp. nectar. A study of the subdivision of this resource by the species revealed 2 strategies. Allen establishes small

feeding territories containing a high density of flowering *Zauschneria* and Anna uses large feeding territories with a low density of food plants. Analysis of feeding behavior indicated that Allen feeds more frequently and for shorter periods of time than does Anna. These differences in feeding strategy and choice of feeding territory are likely the results of differences in crop size and variable nectar renewal rates.

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