

THE CONDOR

VOLUME 58

NOVEMBER-DECEMBER, 1956

NUMBER 6

ECOLOGIC OVERLAP OF ALLEN AND ANNA HUMMINGBIRDS NESTING AT SANTA CRUZ, CALIFORNIA

By KEN LEGG and FRANK A. PITELKA

If different species of birds or other animals overlap in their occupation of habitat, and if their requirements are more or less similar, there is reason to expect that they may compete. To study such competition in natural populations, it is necessary to gather evidence on aggression between members of the respective species, on their density levels and shifts in populations, and on related matters. These are rather large objectives considering how difficult it is to deal with such problems in the field. Nonetheless, it was thinking along these lines that motivated this study of nesting Allen and Anna hummingbirds (*Selasphorus sasin* and *Calypte anna*) at Santa Cruz, California, from November, 1953, through the breeding season of 1955.

That there may be reduction of densities of breeding males of these two species in areas of overlap has already been reported (Pitelka, 1951*b*). For females, information is lacking. They nest in habitats different from those occupied by breeding males; and as no pair-bond is formed, nesting sites show no consistent relation to display territories of males (Pitelka, 1942). The nesting of the Allen Hummingbird has been studied in some detail (Aldrich, 1945), and the fact of overlap in the activity of nesting females of the two species is also known (Pitelka, 1951*a*). However, to date no serious attention has been given to the interrelations of nesting females on areas where both species occur.

This paper is based on observations in such an area. Because the field work had to be terminated after two years, the results are only preliminary and suggestive. Although the main stress is placed on data concerning females, the territoriality, aggressive behavior, and relative abundance of males are reported when they add significantly to the local picture or to information available in the literature.

All field work was carried out by Legg, and the first draft of this paper was prepared by him. The study was planned and carried out with suggestions from Pitelka, who then collaborated in the preparation of data and text for publication. The final versions of the maps shown in figure 1 were prepared by Mrs. Lois C. Stone, to whom the authors express their gratitude.

STUDY AREA

The study area, about six acres in size, included an entire small canyon located in the Natural Bridges State Park, Santa Cruz, California, at the north end of Monterey Bay. This canyon runs approximately north and south, and it varies in elevation from ten feet above sea level in the bottom to fifty feet at the rim. Both the north and south ends are bounded by city streets.

The length of the canyon is 1200 feet. The area was divided into twelve equal sectors of 100 feet each to facilitate accurate plotting of nest sites. The width of the canyon increases gradually from 100 feet at the north end to 450 feet at the widest point (fig. 1). A winter stream carries run-off water from the hills to the north. This stream forms a pond at the south end of the canyon which gradually dries up in late summer and refills in winter. It always contains water through the breeding season. The south

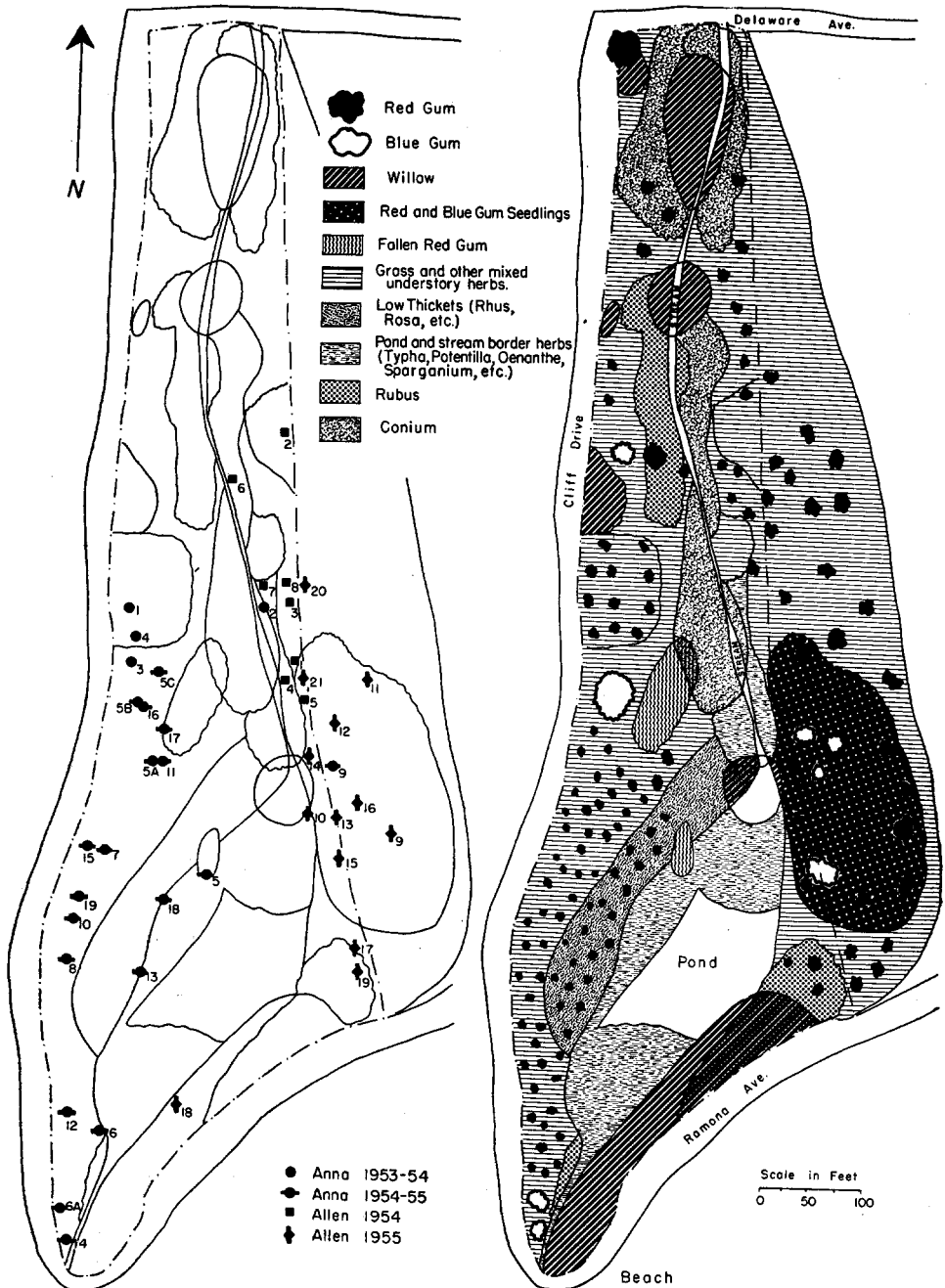


Fig. 1. Right, map of East Canyon, Natural Bridges State Park, Santa Cruz, California, showing approximate distribution of the chief vegetation types. Left, locations of nests of the Anna and Allen hummingbirds found in two successive seasons.

end of the canyon opens out onto a sandy beach with scattered, low clumps of willows. The south boundary of the study area is six hundred feet from the ocean shore.

Eucalyptus of two species, *Eucalyptus globulus*, hereafter referred to as blue gum, and *Eucalyptus amygdalina* or red gum are the only trees present except for groups of *Salix*, most of which are confined to the canyon bottom (fig. 1). Both species of hummingbirds use eucalyptus trees and bushes more than any other plant; this use includes perching, feeding, and nesting.

To the south on the study area, approximately one-half of the west slope is covered by red gum (fig. 2). These trees, many of which are multi-stemmed, are stunted because of shallow soil on the underlying shale, and few have grown beyond a four-inch diameter. They are fairly closely spaced, averaging six feet apart. The average height of these spindly trees is thirty feet. It was here that most of the nests of the Anna Hummingbird were found (figs. 1 and 2). Two large blue gums grow in this area. The northern half of the west slope supports a mixture of widely spaced red gums, several blue gums, willow clumps, and open areas occupied chiefly by *Conium* or *Rubus*.

On the east slope, the northern one-third supports relatively few trees, but near the center of this sector is a group of red gums most of which are large in diameter (8–10 inches) and 40 to 60 feet tall. There is an extensive group of willows in the north-central sector. East and north of the pond is a group of willows bounded by several large blue gums. Around these parent trees, and covering an area of about one hundred square feet, is a close-set group of blue gum seedlings. Most of the nesting area of the Allen Hummingbirds was confined to this section (fig. 3). Over these seedlings, larger trees of red gum form an upper story. The extreme south end is dominated by willow with *Rubus* as an understory.

SEASONAL OCCURRENCE AND POPULATION LEVELS

The first hummingbird that could be regarded as a breeding or potentially breeding individual was noted in the area on December 9, 1953, when a male Anna was heard singing from a perch forty feet up in a flowering blue gum. On December 18 a pursuit between a male and a female Anna was observed, and on the 25th a female was gathering nest material. One or two Anna Hummingbirds were probably present in the area throughout the year, but there was a decided influx of females around January 1, 1954.

In the same season, 1953–54, the first Allen Hummingbirds, both a male and a female, were seen on February 8. After nesting, Allen Hummingbirds appear to leave the canyon early, possibly due to the scarcity of flowering plants. The last Allen was seen in the study area on August 8, but one was seen in Santa Cruz nearby as late as October 3.

On April 1, 1955, a careful estimate was made of the numbers of both species. The population at that time was thought to be about five females of *anna* (breeders or potential breeders), and no males, except birds of the year. At least two adult males were present on the outskirts of the study area, and they may have come into the canyon periodically. Of *sasin*, fifteen breeding females and seven adult males were present, and possibly a few young. Males were easily and accurately counted due to their presence in established territories and their habit of holding prominent, regularly occupied perches.

Thus, the breeding density of the two species of hummingbirds together on the study area may be estimated at 27 individuals on six acres or, converted to a standard expression of density, 450 per 100 acres. It is evident from the preceding remarks regarding young and the occasional visits of adult males of *anna* that this is a minimal estimate of the total numbers present.

The number of nests found in the two breeding seasons is not an accurate basis for

estimating populations of females of the two species, as, from the first year to the second, success in location of nests improved considerably. For the Allen Hummingbird, there were more females in 1953–54 than in 1954–55; but for the Anna Hummingbird, the situation was reversed, and there were more females in 1954–55 than in 1953–54.



Fig. 2. Area of red gum on west side of canyon in Natural Bridges State Park; this was the main nesting area of the Anna Hummingbird.

In the two breeding seasons together, 44 nests were found in the study area, 23 of *anna* and 21 of *sasin*. In 1953–54, four *anna* and eight *sasin* nests were found; and in 1954–55, 19 *anna* and 13 *sasin* nests were recorded (table 1). These figures include all located nests, and hence also the successive nests of certain individual females.

In 1953, the first *anna* nest, then under construction, was found on December 29; in 1954, the first nest, in beginning stages of construction, was found one week earlier, on December 22. *Calypte anna* has young by the time *Selasphorus sasin* arrives. On February 8, 1955, an Anna Hummingbird was feeding young at nest 5C.

NESTING HABITATS

The types of nesting sites used by the two species on the study area are shown in figures 2 and 3. *C. anna* chose, almost exclusively, the more open west slope where tall red gum trees were predominant. By contrast, *S. sasin* often utilized as nest sites the more dense, less illuminated area of blue gum seedlings. Some nests (about one-half), however, were in situations similar to those of *anna* but on the east side of the canyon.

Nests of *anna* were placed higher than those of *sasin*, the lowest *anna* nest being ten feet above the ground. One *sasin* nest was 18 inches from the ground. Average

height of *sasin* nests was 18.5 feet; average height of known *anna* nests was 27.5 feet, and the actual figure is probably higher. Nests of *anna* were all in red gums. Nests of *sasin* were 42.8 per cent in blue gum, 47.6 per cent in red gum, 4.8 per cent in *Salix*, and 4.8 per cent in *Rubus*.



Fig. 3. Area of blue gums, including parent trees and many seedlings; this was the main nesting area of the Allen Hummingbird.

NEST BUILDING

The length of time required for completion of the nest in *anna* varies. Early nests, in December and January, are built more slowly; the time may occupy a month or more. One nest was built in two days. On February 24, 1955, the first down of this nest was placed. On the 25th, the nest was a cup with green lichens on outer walls. At 1:00 p.m. on February 27 the bird was incubating two eggs. At this nest, when building was under-way, trips with material were made every 20 or 30 seconds.

Locations of early nests of *anna* are frequently changed. In some instances at least, this is brought about by bad weather. In the first season, from suggestive observations on one female, we could only speculate that she was shifting the location of her nest. Closer watching the following year, however, removed all doubt. Female 5 of *Calypte anna* (table 1) moved her nest location three times before she found one at which nesting then proceeded.

In 1954, the first nest (number 5 of table 1) was begun probably on the morning of December 22. On December 25, what was apparently the same bird was seen in the act of taking material from this nest and moving it to another site (5A). On January 3, she was taking this newly placed material to still another location (5B), 40 feet away. A

Table 1
Dates, Locations, and Fates of 44 Nests of Hummingbirds

Species and season	Nest no.	Date found	Stage when found	Date nest completed	Fate	Plant cover	Height in feet	Successful
<i>C. anna</i>								
1953-54	1	Dec. 29	Building	Jan. 9	?	Red gum	?	No
	2	Jan. 22	Completed	Feb. 13	Destroyed by storm	Red gum	40	No
	3	Jan. 30	Building	Feb. 26	Destroyed	Red gum	20	No
	4	Feb. 21	Completed	Apr. 8	Young fledged	Red gum	25	Yes
1954-55	5	Dec. 22	Just begun	Dec. 24	Moved	Red gum	20	No
	5A	Dec. 25	Building	Dec. 31	Moved	Red gum	40	No
	5B	Jan. 3	Building	Jan. 5	Moved	Red gum	?	No
	5C	Jan. 8	Building	Feb. 27	Young fledged	Red gum	20	Yes
	6	Dec. 25	Building	Jan. 5	Nest not completed	Red gum	40	No
	6A	Jan. 11	Completed	Feb. 1	Young fledged ?	Red gum	50	Yes ?
	7	Feb. 8	Nearly completed	Mar. 27	Young fledged	Red gum	20	Yes
	8	Feb. 24	Just begun	Mar. 16	Deserted	Red gum	15	No
	9	Mar. 13	Building	Apr. 29	Young fledged	Red gum	10	Yes
	10	Mar. 22	Building	?	?	Red gum	25	No
	11	Mar. 23	Incubating	Apr. 18	Young fledged	Red gum	25	Yes
	12	Mar. 26	Building	Apr. 5	?	Red gum	30	No
	13	Apr. 12	Building	?	?	Red gum	?	No ?
	14	Apr. 29	Nearly completed	?	?	Red gum	25	?
	15	Apr. 30	Building	?	?	Red gum	25	?
	16	May 4	Half-built	?	?	Red gum	30	?
	17	May 14	Completed	May 21	Abandoned	Red gum	35	No
	18	May 24	Completed	?	Young fledged	Red gum	25	Yes
	19	June 8	Incubating	?	Young fledged ?	Red gum	30	Yes ?
<i>S. sasin</i>								
1954	1	Feb. 21	Just begun	Apr. 28	?	Red gum	30	?
	2	Feb. 28	Eggs ?	?	?	Red gum	35	?
	3	Mar. 13	Incubating	Apr. 8	Young fledged	Blue gum seedling	4	Yes
	4	Mar. 13	Nearly completed	Apr. 18	Young destroyed	Blue gum seedling	4	No
	5	Mar. 13	Just begun	?	Nest not completed	Red gum	20	No
	6	Apr. 12	One egg	?	Destroyed	Blue gum seedling	10	No
	7	Apr. 12	Completed	?	?	Red gum	20	?
	8	Apr. 14	Incubating	Apr. 19	Destroyed	Blue gum seedling	?	No
1955	9	Mar. 1	Completed	?	Probably destroyed	Red gum	20	No
	10	Mar. 1	Just begun	Mar. 18	Deserted	<i>Salix</i>	25	No
	11	Mar. 11	Just begun	Apr. 18	Young fledged ?	Red gum	20	Yes ?
	12	Mar. 11	Just begun	Mar. 13	Abandoned	Red gum	25	No
	13	Mar. 15	Building	Mar. 18	Fell down	Red gum	25	No
	14	Mar. 15	Just begun	Mar. 22	Abandoned	Blue gum seedling	20	No

Table 1 (continued)

Species and season	Nest no.	Date found	Stage when found	Date nest completed	Fate	Plant cover	Height in feet	Successful
	15	Mar. 15	Completed	?	Young fledged ?	Blue gum	30	Yes ?
	16	Apr. 2	Just begun	Apr. 4	Abandoned	Blue gum seedling	10	No
	17	Apr. 7	Half completed	Apr. 10	Abandoned	Red gum	25	No
	18	Apr. 20	Half completed	June 5	Young fledged	<i>Rubus</i>	4	Yes
	19	May 11	Incubating	May 27	Destroyed	Blue gum seedling	1½	No
	20	May 15	Building	May 18	Nest not completed	Red gum	40	No
	21	May 16	Incubating	May 27	Destroyed	Blue gum seedling	2½	No

strong wind broke one of the twigs supporting the nest and caused it to tilt. At the time of the accident nest 5B appeared to be completely built. On January 8, she was watched taking material from this nest and transporting it to another site 20 feet north of 5B, to location 5C. January 15 through 19 were cold rainy days with ice on puddles in the mornings. By this time nest 5C contained eggs; the incubating female huddled low in the nest and was not seen to go for food at any time when rain was falling. On February 8 she was feeding young.

This female *anna* was not marked but it was apparent that she was one and the same bird. She was then the only female in the area. Although another was nesting, and also made one nest-location shift, in the south end of the canyon, this was some distance away, and many hours of observation each day permitted Legg to become familiar enough with the first female's movements and behavior to be reasonably sure that it was the same individual.

No nest-building in the Allen Hummingbird was observed at length, but both species appear to have similar methods of building. Several nests of *anna* were found when first, or near-first, material was placed. A wad of down was set on a limb, then bound with spider webs. Material brought to the nest consisted of webs or down. Usually these trips were made so that down was brought on three or four successive ones, then webbing on two or more successive ones, then down again, and so forth.

Nest building begins shortly after morning feeding, which occurs early, just after daybreak. It continues at an active pace until about eleven o'clock, then slowly comes to a standstill in the afternoon.

Some Californian naturalists believed they could identify the species of hummingbird responsible for a nest by structural features of the nest. In an area where both Allen and Anna hummingbirds nest, this may be true. Here, at Santa Cruz, most Allen nests were composed of brownish materials, whereas Anna nests were white, or gray. Anna nests, in the main, were smaller, and more shallow; Allen nests were usually taller and more bulky. There were, however, exceptions to this, some Anna nests being quite long and also bulky.

These structural differences seem to be correlated with the type of nest location. For the most part Anna nests were pad-like cups placed upon large solid surfaces. Those which incorporated, or were built upon, twigs usually were of similar size and shape to those of the Allen Hummingbird.

Color differences in nest structure are the result of different materials used. The Allen Hummingbird used bits of shredded eucalyptus bark, whereas the Anna Hum-

mingbird used some shredded fibers from the gray-colored stems of dead herbaceous plants such as the bristly ox-tongue (*Picris echioides*). Most Anna nests were composed mainly of cattail down. A few early Allen nests included the same material until willow down became available.

No examples of re-use of the nest structure were observed, nor was a new nest ever seen to be constructed on top of an old one. Old nests, by the time young depart, are badly disheveled and probably unusable. However, in many cases the materials are transported to another location and re-used.

A nest being dismantled assumes the appearance of an apple being pared down by a peeler going around and around until nothing remains. The bird hovers beside the nest and works around the cup, jabbing at it and pulling backward from it until the walls are demolished. Then the pad is taken bit by bit.

It was relatively easy to speculate which females of either species were re-nesting. If the old nest disappeared a few days after young were fledged, it was thought that a second nesting was underway. Only near the end of the nesting season were old nests not utilized. If the original owner did not use the material from previous nests, other hummers discovered and used it in spite of the fact that webbing and down were much in evidence in the area.

TERRITORIAL RELATIONS AND AGGRESSIVE BEHAVIOR OF FEMALES

The nesting density of females was lower in *anna* than in *sasin* (fig. 1). In early March, 1955, four females of *anna* (6A, 7, 8, and 9; see table 1) were active, but the last female on the scene (nest 9) was forced to invade *sasin* territory (fig. 1). Nests of females 7 and 8 were then known; a third female considered to be 6A was also present then, but its nest, if it had one, was not located. Nests 10 to 12, representing three concurrently established *anna* females, were separated from each other by approximately two hundred feet.

Note the grouping of *anna* nests shown in figure 1. It is believed that each group represents but one female, all nests in the area having been constructed by the same individual, except that nest 5 belongs in the group containing 5A, 5B, and 5C. Nests 13 and 17 may have been built by another individual, thus setting the total number of breeding females at five. These comments refer to the nests of 1955. The interpretation is strengthened by the fact that there was but one active nest in each group at any one time.

Also in March of 1955, seven females of *sasin* (numbers 9-15 in table 1) had, or were building, nests all of which were within an area no greater than 200 feet long and 100 feet wide. But when Anna 9 moved into the territory, Allen 12 was forced to vacate. This was a case of an Anna female displacing an Allen female. No examples of Allen females moving into Anna territory were recorded.

One Allen nest was built in a willow that was barren of leaves. As buds began to burst and down became available, it was the most popular place in the canyon for material-gathering Allens, and often three or four would be in the willow grove at the same time. The local incubating female seemed almost to become frantic. Each time an intruder seeking nest material appeared, she left her nest and drove it off, but there was always at least one present. Her zone of defense was a 30-foot circle about the nest. Sometimes birds beneath the nest went unmolested, but all those above or on a level with it were driven off. So busy was she kept driving other females away that she deserted her eggs after one week.

One persistent case of thievery was observed. One Anna was building a nest, and each time she was absent another Anna would come and take away material. Once the

rightful owner arrived when the intruder was present and drove her off. This seemed to put an end to the thieving, for the nest was completed successfully.

In the early part of the breeding season, before Allen Hummingbirds arrive, there is little indication of quarreling among Anna Hummingbirds. Later, after the former species arrived, female Annas were often seen gathering nest material or feeding in the nesting area used by Allens. To a lesser degree female Allens penetrated Anna territory for food.

Why was it that no female Allens attempted to utilize the west side of the canyon? Was it because the terrain, exposure, vegetation and other features were not suitable, or was it because Anna females were already established here? Allen females visited the nesting area of Anna females only seldom, and those which did stray into this area were set upon and put to route. Anna females seemed to visit Allen nesting territories at will, both to feed and to gather nest material. Such intrusions were more frequent than the reverse, but nonetheless Anna females were occasionally pursued by nesting Allens.

In general, activity of Anna females spilled over into the main nesting area of Allen females more than the reverse. Also, it appeared that, given an instance of intrusion, an Allen female was less likely to escape a chase from an Anna territory than in the reverse situation. However, it is not possible to assume that Allen females would utilize the nesting area claimed by the Anna Hummingbird if the latter were absent. The usual nesting and feeding sites of Allen females fall outside of the Anna nesting area. Hence the intrusions of Allen females into such an area may best be considered merely incidental, conspicuous though an ensuing chase may be.

Among females, instances of *anna* driving *sasin* out of nesting territories were recorded in 1955 on February 25, March 15, and May 4; in addition, on April 18, a female *anna* pursuing a female *sasin* from the west slope was probably an example of the same situation. For *sasin*, we have records of females driving females of *anna* out of nesting territories on March 11, March 23, April 20, and April 29. On March 29, an *anna* female was seen pursued by two females of *sasin*. These are records of chases in which the participants were satisfactorily identified, but the figures of four instances in favor of *anna* and five instances in favor of *sasin* mean little, not only for the reasons given above, but more importantly for the reason that in many encounters and chases witnessed, the participants could not be identified.

Breeding females of both species were seen to pursue Pileolated Warblers (*Wilsonia pusilla*), Chestnut-backed Chickadees (*Parus rufescens*), Audubon Warblers (*Dendroica auduboni*), and House Finches (*Carpodacus mexicanus*) when individuals of these species came too close to their nests. Both Sparrow Hawks (*Falco sparverius*) and Red-tailed Hawks (*Buteo jamaicensis*) were pursued in mid-air by hummers. On June 17, 1955, at least a dozen Allens and several Annas, all "ticking" excitedly, mobbed a sleepy Screech Owl (*Otus asio*) that perched in a seedling blue gum.

Although most Allen Hummingbirds were belligerent to blundering Chestnut-backed Chickadees which came too close to their nests, one female *sasin* nested within 10 feet of a chickadee's nest with young which was in a knot-hole. The parents made frequent trips to the hole with food, but the hummer paid no attention to them.

OTHER OBSERVATIONS ON NESTING

For 32 nests whose outcome is known (table 1), percentage of success is low, 30 per cent for Anna and 12 per cent for Allen. If the number of nests is increased to 37 to include those that were probably successful, the estimates of nesting success increase to 40 per cent for Anna and 24 for Allen.

In 1954 it was strongly suspected that an Allen was building a nest fifteen feet from

where she was feeding a single young. Both were one-egg nests. A chance actually to observe such dual nesting by an Anna came on March 22, 1955, when Anna 7 had nearly full grown young. This bird was seen building another nest 60 feet distant (nest 10) and making trips to feed her nestlings alternately. Cogswell (1949) reported alternated care of two nests by the Black-chinned Hummingbird (*Archilochus alexandri*).

Anna females were much more at ease on their nests than were Allens, as reported by Aldrich (1945:147). Incubating and brooding Annas were quiet, still, and unaffected by nearby intruders, seeming to depend upon immobility for protection. By contrast, Allen females turned the head, seemed excited, and squealed whenever another hummer came within 100 feet of the nest.

TERRITORIAL RELATIONS AND AGGRESSIVE BEHAVIOR OF MALES

No special attempt was made to study the displays of the two species. Due to the height at which most of this activity occurred and to the screening effect of the vegetational canopy, little was seen of this phase of the Anna Hummingbird's behavior. Also, males of this species were relatively scarce on the study area after January. However, observations on territorial and display behavior considered to be of interest are reported here.

The male Anna Hummingbird may begin its territorial displays in November. On November 6, 1954, a male was heard diving, and a few seconds later it was observed in pursuit of a female.

On several occasions when females of *anna* were observed constructing their nests, males were seen to come within a foot or so of the nest. These visits by the male always terminated in a pursuit, sometimes by the male, at other times by the female. These occasions produced longer absences from the nest than any other activity of the female.

After January, and more particularly after males of the Allen Hummingbird arrived, adult males of the Anna Hummingbird were present regularly only on adjacent uplands with open brush cover.

In the Allen Hummingbird, both sexes were usually much in evidence in the canyon bottom, and frequent opportunity was afforded to witness their activities closely. In this species, territorial display and mating begin as soon as the males arrive. Unlike the Anna males which came to nest sites in the course of construction, I witnessed only one male Allen in a nest territory when his presence was not the result of feeding or incidental passage through the area. This occurred on April 27, 1955: A female was seen to go to a perch about ten feet from her nest. She may have spotted a cruising male, for she gave one squeal. The male immediately appeared and began to display above her.

By the last of April displays and pursuits of the Allen Hummingbird subside. Aggressive behavior declines decidedly after May 15. After this time, weak and more or less incomplete flight displays are seen. Any portion of the display may be omitted. A pendulum may be executed without the terminal tail-movements and "clicking." Pendulums may be executed over females but may not be followed by "towering," the male merely flying off to a perch. Silent pendulum display-flights are common after June first. The last date on which I saw a silent pendulum flight of a male over a female was July 8. Later she made several trips with nest material to a site, but the nest was never completed. On April 24, 1955, a female *sasin*, accompanied by a fledgling, supposedly her's, set off a display when she and her offspring appeared in a male's territory.

Among Allen males, there appeared to be two types of territories in the study area, one for feeding, the other for prenuptial display and mating. Feeding territories were small, many in number, and usually the scenes of much confusion and contesting. A

single large blue gum at the height of the flowering season may provide four or five rather loosely held, defended areas. Here territories may even be vertically distributed, and a single large limb with a profusion of blossoms may constitute a territory held by one individual for a week or more. It is practically impossible to unravel the activities about such situations.

Breeding territories are more formally established, readily defined and easily observed. Indeed, in many cases the defending male may occupy the same perch day after day, although alternate perches may be used under different weather conditions. For example, on a warm, sunny day, the perch may be the top-most branch of a willow, the highest perch in the territory; on drizzly or foggy days, the perch may be under a canopy of over-hanging leaves in a red gum tree.

Adjacent territories of male Allen Hummingbirds are usually sharply defined. In the Natural Bridges canyon there were three territories in a row, each separated from the other by vegetational screens. These were located in the north end where there was no nesting activity. However, other males were located above nesting areas, in and around the tops of tall blue gums. One male Allen set up a territory just north of the pond (fig. 1) and directly between two nesting territories, one held by a female *anna*, the other by a female *sasin*. He had a small open area not over 50 feet in diameter in which he successfully maintained his position.

At times, territorial males do not react as expected. Although they are usually quite efficient at sighting and routing an intruder, instances are recorded where an outsider appeared, but, for some unknown reason, was not pursued. On February 23, 1955, Legg witnessed such an incident: One male Allen was feeding, probing damp willow leaves, presumably for insects. Presently a second male came into the area. Both flew to and perched on dead *Conium* stalks about six feet above the ground and ten feet from each other. Ordinarily a clash would occur, but here neither bird reacted. Presently one flew down the canyon, and the other returned to his feeding. Some males seemed never to become established but frequented the feeding areas and were found generally through the area.

About the middle of April, overall activity began to increase in the north part of the canyon as young of the year began to appear. At this time, and perhaps because adult males were less aggressive than a month or two previously, few of these young seemed to be molested. They succeeded in remaining in the area, and although there may have been some instances of young being driven out by established adults, none was witnessed.

On April 26 a young *anna* male settled on a small territory on the canyon slope below nesting territories of *anna* and defended it successfully against all comers until early in June. From his perch he poured out his squeaky, juvenal songs, and if any other hummer, of either species, entered this *Stachys* patch he was quickly chased.

Several records of territorial conflict between males of the two species were obtained. At Point Lobos Reserve, in Monterey County, on February 17, 1953, an Anna male was securely established in a territory overlooking a chaparral-covered slope. His constant perch was a specific twig of a *Ceanothus* bush. A female was seen gathering nest material in the near vicinity on the same date, and later a nest was found in pines not far away. Here were Anna hummers of both sexes, possibly a mated pair, established in a given area. But, on March 7, a male *sasin* occupied the same area and even the identical twig, keeping the territory throughout the summer.

On January 16, 1954, a male *anna* had a territory at the north end of the study area. He was observed here daily, where he perched in the top of a red gum and sang. On February 16, I observed a violent clash between him and a male Allen. The Allen chased the male Anna into a clump of willows from which came the sounds of chattering, squeal-

ing and the actual clash of wings. Presently the Allen came out, but the Anna was not seen to emerge. The following day, an Allen male had control of the north part of the canyon while an Anna was perched on a lone *Baccharis* shrub surrounded by an open field more than 100 yards away from the perch occupied earlier. The Anna male remained in the field all summer and, as far as I am aware, never challenged the Allen. Still another Anna which formerly had territory in the canyon withdrew to an open area to the eastward and likewise settled on a *Baccharis* bush shortly after Allen hummers arrived.

Trousdale (1954) states that "for the first time in our garden an Anna Hummingbird [male] succeeded in banishing an Allen Hummingbird [male]." Pitelka (1951*b*) also has indicated that *anna* may be successful in conflicts between males of the two species. In our experience at Santa Cruz, males of *sasin* consistently banish males of *anna* from territories. Pitelka (1951*b*) earlier has observed three instances of apparent displacement of *anna* males by *sasin* males. The reverse may be true between females of the two species, or at any rate, females of *anna* were secure in their nesting area and were seen regularly in the nesting area of *sasin*. If these opposing trends on the study area are real, they may balance each other, and there may be little margin of success favoring either species.

FEEDING

There were few flowering plants in the study area except the profusion of blue gum blossoms in the early part of the season. Both species of hummers were seen probing flowers of mustard, radish, blackberry, vetch, poison oak, hedge nettle, lupine, and morning glory. In early morning and late evening, when small flying insects could be seen in the air, many hummers were observed flying out and taking these.

On two occasions *anna* females were seen on the ground. Both appeared to be feeding. The tongue came into view repeatedly, and the throat muscles were also seen to move as though the bird were swallowing. Once the hummer was at a gravelly place; on the other occasion it was at an ash pile where brush had been burned. After watching what appeared to be feeding, I intentionally flushed the birds and immediately went to the sites to determine what it might be they were seeking. In both cases small ants were present at the spot where the birds had rested.

From the middle of April, and then throughout the summer, males and females of both species were frequently seen taking white flies (*Aleyrodidae*) from the foliage of *Rubus*. On May 15, 1955, I watched closely a young *anna*, which came within three feet of where I sat; it was feeding on white flies which covered the leaves of one of these berry bushes. Some of the insects adhered to the sides of the bill.

SUMMARY

Breeding populations of Allen and Anna hummingbirds (*Selasphorus sasin* and *Calypte anna*) were studied near Santa Cruz, California, in 1954 and 1955. The study area, about six acres in size, was a long narrow canyon in which the chief habitats were eucalyptus groves, willow thickets, and open areas with brush, tall herbs, and scattered eucalyptus trees.

The breeding population, on April 1, 1955, was estimated at five females of *anna* and 15 females and seven males of *sasin*. In 1954, while a population estimate was not obtained, it was known that there were more females of *sasin* and fewer of *anna*.

In these two years, 44 nests were found, 23 of *anna* and 21 of *sasin*. Early nests of *anna* may be moved as much as three times before the nesting gets underway. Building of early nests in *anna* may occupy a month or more; later nests may be built in no more

than two days. Nests of *anna* simultaneously active were spaced about 200 feet apart, whereas for *sasin* nesting density was higher, reaching seven females with simultaneously active nests on one-half acre.

Nesting success was at least 30 per cent in *anna*, but it was only 12 per cent in *sasin*; if additional nests which may have been successful are included, these figures increase to 40 and 24, respectively.

Males of the Allen Hummingbird held two types of territories in the breeding period, the relatively fixed mating territory already well described in the literature and a feeding territory variable in size and in period of occupation. Adult males of *anna*, supposedly territorial, occurred on the study area in November, December, and January; but after *sasin* arrived, they were present only on adjacent uplands with open brush cover.

In all of three instances of satisfactorily observed competition for territories among males, *sasin* displaced *anna*. Between females competing for nesting territories, one instance of displacement of *sasin* by *anna* was recorded, but none was noted showing the reverse. Territorial aggression by *anna* toward *sasin* and the reverse occurs in females as well as in males. On the study area, males of *sasin* were successful in displacing males of *anna*, and females of *anna* were able to hold their own against more numerous females of *sasin* and even to displace an occasional one. On this basis, it is suggested that in such coastal localities as exemplified by the study area, there may be little margin of success favoring either species in their overlap and competition with each other.

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