HYBRIDS OF THE ANNA AND ALLEN HUMMINGBIRDS

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In the course of a recent study of the Anna Hummingbird (Calypte anna), a hybrid between that species and the Allen Hummingbird (Selasphorus sasin) was obtained. This individual, an adult male, was collected by Jerry C. Russell on May 20, 1955, in Woolsey Canyon, Alameda County, California. The canyon, a portion of the University of California campus, is situated on the west side of the Berkeley Hills. It is inhabited by the Anna Hummingbird throughout the year and by both species in the breeding season.

The Anna and Allen hummingbirds overlap in breeding distribution along the coast of California from Ventura County to the San Francisco Bay region (Grinnell and Miller, 1944). To a lesser extent, they overlap also in habitat distribution. In Woolsey Canyon, and in other areas in the Berkeley Hills where the two occur together, males of C. anna are typically found on the chaparral-covered slopes or in chaparral mixed with broad-leafed woodland of open character, while males of S. sasin more commonly frequent the riparian habitat along stream courses in areas of dense shrubbery, willow and laurel (Pitelka, 1951:643, 646; Williamson, 1956). Females of both C. anna and S. sasin nest in habitats other than those in which the males hold territories, and here again there is ecologic separation (Grinnell and Miller, 1944:220, 222). In the Berkeley Hills females of C. anna usually nest in live oak woodland, while those of S. sasin nest in oak-laurel woodland, in understory shrubs such as blackberry, and in thickets of shrubs or areas of mixed tall, soft and broken chaparral (Pitelka, 1951:647).

At the onset of nesting, females of *C. anna* and *S. sasin* enter the territories of the males (Williamson and Pitelka, MS). Due to the overlap in ecologic distribution of the males, ample opportunity is afforded for mixed contacts between males and females of these two hummingbirds, resulting apparently in occasional hybridization. Other behavioral and morphological factors that might seem predisposing to interbreeding also exist; these will be discussed later.

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DESCRIPTION OF THE HYBRID

The hybrid most nearly resembles C. anna, but notable differences were found in the color, form, or both, of the feathers of the capital, ventral, alar, and caudal tracts. Certain dimensions fall within the range of both species while others are intermediate.

Capital tract.—In C. anna the iridescent red feathers of the throat (gorget) extend onto the crown and cover the entire frontal region to a point well back of a line drawn between the mid-point of the eyes. This extension of specialized feathers is not present in S. sasin. The hybrid possesses a lesser number of such feathers covering most of the frontal region but terminating at a line drawn between the mid-point of the eyes. The color of these feathers in the hybrid is intense red, much as in C. anna, although at the base of the bill they assume a rufous tinge. Across the base of the upper mandible is a fine edging of small, rufous feathers that is lacking in C. anna. This rufous color extends posteriorly, covering the entire loral region and to a lesser extent the superciliary region. The circlet of feathers around the eye is also rufous. In C. anna, the loral, superciliary and ocular regions are grayish in color, some of the feathers possessing whitish tips.

Ventral tract.—The feathers comprising this tract are for the most part like those of C. anna. The gorget is similar in all respects but color. It covers the interramal, malar and submalar regions, and the outer posterior feathers, or "tails," are well developed, extending posteriorly as in C. anna. At the base of the lower mandible is a fine line of rufous feathers not present in C. anna. The entire gorget is washed with a rufous tinge similar to that of S. sasin. As mentioned earlier, this tinge is not apparent

over most of the red feathers that extend onto the crown. The cervical region is like that of *C. anna*, being composed of feathers that are basally grayish and tipped with dusky white. The feathers of the sternal, axillar, and abdominal regions are, as in *C. anna*, gray basally, green for the outer third, and tipped with white. However, they show a distinct rufous wash as in *S. sasin*. This is most pronounced in the sternal region near the base of the wings.

Alar tract.—The general form and coloration of the wings are like those of *C. anna*. The rufous feathers of the sternal region extend onto the wing and all the under secondary coverts are this color. The marginals are also rufous. The outer primary is more slender than that of *C. anna* and slightly incised along the trailing edge. All the primaries are shorter and more slender than in *C. anna*. The secondaries and their greater coverts are as in *C. anna*.

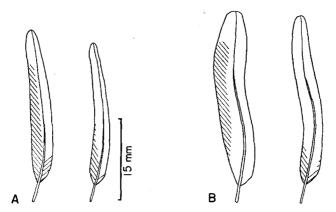


Fig. 1. A, outer two left rectrices of Selasphorus sasin x Calypte anna hybrid; B, corresponding rectrices of C. anna. Shaded areas indicate distribution of rufous in hybrid and gray in C. anna, respectively. Gray areas at base of outer (narrower) rectrix in anna (B) actually merge gradually with black distally.

Caudal tract.—Unfortunately all but the outer two rectrices on the left side were lost at the time of collection. These remaining two feathers, however, are quite different in most respects from those of both C. anna and S. sasin and merit description. The tail of C. anna is emarginate whereas that of S. sasin is rounded. The outer rectrix remaining on the hybrid is shorter than the inner feather and thus suggests the tail form of S. sasin. In shape it is somewhat similar to that of C. anna, although it is shorter, more slender, and pointed. The base is rufous and the outer portion grayish black. The inner of the two rectrices also somewhat resembles that of C. anna, although again it is more slender and pointed like that of S. sasin. A large portion of the inner web and a smaller portion of the outer web is rufous. The rufous of this last feather extends over much of the same region that is grayish in the corresponding rectrix of C. anna. The remainder of the feather in C. anna is very nearly black. The distribution of color on these feathers and a size comparison with the corresponding feathers of C. anna are shown in figure 1. Aldrich (1956:125) presented a figure comparing the tails of C. anna and S. sasin.

Mensural characters.—Linear measurements of a series of males of C. anna and S. sasin collected in the San Francisco Bay region are presented by Pitelka (1951:643), and these can serve as a basis for comparison with the hybrid. This comparison is made in table 1. It can be seen that the hybrid is intermediate in length of wing, falling between the non-overlapping ranges of the species. The length of the culmen is well within the range of both species although slightly nearer the mean for S. sasin. As indicated by Pitelka (1951:642), C. anna and S. sasin differ very little in bill size and form. In weight the hybrid falls in the range of C. anna. These size differences are such that were it not for the presence of the restricted areas of rufous coloration, the hybrid might easily be mistaken for C. anna, as indeed it was when it was collected.

Breeding condition.—Measurements of the left testis were made, and the volume, when computed in cubic millimeters, was found to be 5.4 mm.³ One of the testes was imbedded in paraffin and sec-

Table 1

Measurements of the Hybrid Compared with Males of Calypte anna and Selasphorus sasin1

		Number of specimens	Mean with standard error	Range
Hybrid:	Wing	1		42.5 mm.
	Culmen	1		16.0 mm.
	Weight	1		3.9 gm.
C. anna;	Wing	22	$48.87 \pm 0.16 \text{ mm}$.	47.0-50.1 mm.
	Culmen	22	$17.06 \pm 0.16 \text{ mm}$.	15.9-18.3 mm.
	Weight	7	4.00 gm.	3.3- 4.7 gm.
S. sasin:	Wing	15	$38.26 \pm 0.11 \text{ mm}$.	37.5-39.1 mm.
	Culmen	12	$15.83 \pm 0.16 \text{ mm}$.	14.9-16.9 mm.
	Weight	7	3.10 gm.	2.7- 3.6 gm.

¹ All specimens collected in the San Francisco Bay region.

tioned for analysis of histologic condition. The testis was in breeding condition and appears the same as *C. anna* at a similar stage (Williamson, 1956). Bundles of sperm were arranged, with their heads pointed outward, around the lumina. Some sperm were free in the lumina.

REVIEW OF OTHER KNOWN HYBRIDS

The hybrid described in this report represents the fifth such specimen recorded in the literature (Grinnell and Miller, 1944:569; Cockrum, 1952:145), and it is the fourth definite record for California. In all probability, the first recorded hybrid described by Gould (1861:pl. 139) as Selasphorus floresii was also taken in California. The type locality of S. floresii, although given as Bolaños, Oaxaca, México, should be Bolaños, Jalisco, as pointed out by Ridgway (1909:440). Ridgway stated the belief that the collector, Floresi, obtained specimens in California which were subsequently mislabeled Bolaños.

The four hybrids collected in California were all found in the San Francisco Bay region, and the localities where they were collected are shown in figure 2. A male was taken near San Francisco in May, 1885 (Bryant, 1886), another male at Hayward, Alameda County, in February, 1901 (Emerson, 1901), and a third individual, the sex of which is not indicated, in February, 1908, in the vicinity of Nicasio, Marin County (Taylor, 1909). This third specimen was evidently a male as it possessed all the plumage characteristics of that sex.

Bryant (1886:426) gave no description of his specimen, and although he felt that it possibly represented a hybrid, he decided, on the advice of Ridgway (personal correspondence) to consider it a second example of *Selasphorus floresii*.

Emerson (1901:68) also considered his specimen to be Selasphorus floresii although at the time of collection he thought it might be Selasphorus platycercus. He did not describe it further than to say the rectrices were rufous-edged, the under wing coverts rufous, and the gorget and crown rose-red.

The only description at all adequate for comparison with the hybrid described here is that given by Taylor (1909:291, 292). According to Taylor, his specimen proved nearly identical to the one collected by Emerson. At collection Taylor considered his specimen to be S. "alleni" (here sasin), although in his report, he states the resemblance to be closer to C. anna. His description is very similar to the one given in this paper, with the following differences: a golden tinge is present on all the red feathers of the crown, the breast is whiter than in C. anna, the remaining feathers of the capital and spinal tracts are rufous-edged, the tail is slightly emarginate, and the lateral extensions of the gorget are not so highly developed as in C. anna.

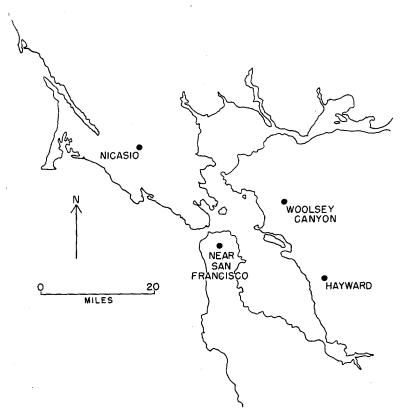


Fig. 2. Outline map of the San Francisco Bay region of California, showing localities where four of the five known hybrids were collected.

DISCUSSION

Taylor (1909:292, 293), and Thayer and Bangs (1907:313), called attention to the proneness of hummingbirds to hybridize. This is supported by the review of known hybrids of North America north of México given by Cockrum (1952:145). This proneness to hybridize would seem to be enhanced by the fact that no pair-bond exists and the fact that in all probability male hummingbirds are polygamous (Pitelka, 1942:195, 201).

Taylor (1909:293), on the basis of the known hybrids between S. sasin and C. anna, questioned the use of feather coloration and form as characters suitable for diagnosing genera of hummingbirds. He maintained that characters of equal rank have been used for separating species in the genera Selasphorus, Calypte (and Trochilus), and he favored combining these genera as one.

Ridgway (1909:440, 441) refuted this suggestion on the basis that *Calypte* differs from *Selasphorus* in possessing an emarginate tail and no trace of rufous in the plumage, and that *Trochilus* possesses a number of characteristics of plumage form and color lacking in the other two genera. He considers the three genera as composing a suprageneric group.

Ridgway's remarks notwithstanding, it appears to me difficult to distinguish satisfactorily the genera Selasphorus and Calypte, either on the basis of morphology or behavior. This seems especially true when other forms such as Selasphorus platycercus

are considered and when the basic similarities of the females are taken into account. The following remarks may lend some support to this view:

In the course of the recent examination of a large number of specimens of *C. anna* for study of the molt process, a small number of males was discovered to have patches of rufous on some of the rectrices. This finding was not recorded in any detail, and the significance it may have is only now apparent. In addition, a number of the specimens I received with the hybrid were more closely examined. Although no member of this small series of 14 males was found to have rufous tail patches, three were found that had a distinct rufous wash on the under secondary coverts and a rufous edging on the marginal feathers of the alar tract. This is faint enough to be easily overlooked.

These findings are contrary to Ridgway's belief that *C. anna* shows no rufous in its plumage. Further, the rufous present is in the same locations as some of that found on the hybrids or on *S. sasin*. The presence of this rufous on only a relatively small number of the males examined might suggest that its presence is not the normal situation and that there was an incident of hybridization in the lineage of the individual showing rufous. The occurrence of this and possibly other characters of *Selasphorus sasin* assumes some significance in view of the fact that the hybrid reported here had a normal testis with mature sperm and hence, was probably a fertile individual. Thus, not only may hybridization be more common than is generally supposed, but there is some reason to believe that the hybrids may be fertile.

Also unknown to Ridgway was the fact that despite the distinct differences in flight displays that occur, there also are certain basic similarities in those of *S. sasin* and *C. anna* (Williamson and Pitelka, MS); also the pterylography of *C. anna*, which I have compared with *S. sasin* (Williamson, 1956), is nearly identical.

Pitelka (1951:641-643) has presented a comparison of the morphological characters of the two species, and in addition points out that the two genera are considered to be closely related. Although the interspecific differences of males are marked, the females differ to a lesser degree. This similarity of females, coupled with the polygamous habits of the males and the overlap in their ecologic distribution, would seem, as mentioned earlier, to render hybridization even more frequent than is now known to be the case.

SUMMARY

An additional hybrid between Calypte anna and Selasphorus sasin is described. This specimen, like the four previously known, resembles C. anna, but it differs primarily in the presence of rufous in the plumage and in certain mensural characters. A review of the other known hybrids is presented and a comparison is made with the hybrid described here.

The generic status of *Selasphorus* and *Calypte* is discussed briefly. There are more similarities between them in morphology and behavior than previously realized. Also, an unknown percentage of *C. anna* males possess rufous in the plumage. The overlap in breeding and ecologic distribution and its possible influence on hybridization is mentioned. Hybridization may occur more frequently than is now known. That these two species should be considered members of different genera, in the light of the present evidence, seems open to question.

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