

# THE CONDOR

VOLUME 63

JANUARY-FEBRUARY, 1961

NUMBER 1

## A REVIEW OF NORTH AMERICAN HYBRID HUMMINGBIRDS

By RICHARD C. BANKS and NED K. JOHNSON

On April 1, 1958, the authors collected a male hummingbird, tentatively identified in the field as *Calypte costae*, in southern Clark County, Nevada. Upon comparison of this individual with various kinds of North American hummingbirds in the Museum of Vertebrate Zoology we realized that it possessed combinations of colors and morphologic characters not typical of any recognized species. The specimen was reidentified as a hybrid between the Broad-tailed Hummingbird (*Selasphorus platycercus*) and the Costa Hummingbird (*Calypte costae*) because it seemed to show the intermediate features one might expect from such a cross. The fact that a hybrid between these species had previously been reported (Huey, 1944) probably influenced this identification. However, subsequent critical examination of the specimen has brought forth evidence which points to the fact that this specimen is the result of interbreeding between the Broad-tailed Hummingbird and the Black-chinned Hummingbird (*Archilochus alexandri*) and that *Calypte costae* was not involved.

A survey of the literature concerning hybrid hummingbirds from North America revealed that such a cross has not been reported heretofore. Two other facts also became evident, first, that most previously reported hybrid specimens have been only briefly and incompletely described, and second, that the number of hybrid specimens does not equal the number of reports of hybrids. The lack of correspondence between specimens and reports has three causes: (1) loss or destruction of hybrid specimens, (2) the listing of more than one parental combination for a single specimen, and (3) the reporting of hybridization without specimen evidence.

The fragmentary descriptions of the previously reported hybrids, the general paucity of information concerning these birds, and the ease with which we misidentified our specimen suggest that re-examination and redescription of the existing specimens of hybrid hummingbirds from North America is in order. Accordingly, we have assembled the seven available specimens of hybrids involving the genera *Archilochus*, *Calypte*, *Selasphorus*, and *Stellula*.

Berlioz (1929, 1930) has pointed out that natural hybridization is merely indicated, not proved, by a specimen showing intermediacy between two well-known species. To this we may add that once a specimen is determined to be a natural hybrid, assumptions as to the parentage of such a bird are also only "best guesses" and cannot, except in rare instances, be established with certainty. The parentage of most natural hybrids is determined under the assumption that hybridization produces no traits characteristic of genera or species other than those involved in the particular cross.

In attempting to ascertain the origins of the hybrid birds discussed here, we have made a second basic assumption, that hybridization occurs most readily where one or both of the presumed parental species is rare. It is believed that low population levels of one or both species can favor hybridization because of the difficulty in finding conspecific mates (Miller, 1955:318; Sibley and Short, 1959:181).

## ACKNOWLEDGMENTS

We wish to thank the following persons for the loan of specimens from their respective institutions: Mr. James C. Greenway, Jr., Museum of Comparative Zoology; Mr. Charles E. O'Brien, American Museum of Natural History; and Dr. Robert T. Orr, California Academy of Sciences. In addition, Dr. Herbert Friedmann and Mr. Laurence M. Huey, as well as Mr. Greenway and Dr. Orr, have contributed helpful information concerning other specimens. Messrs. J. D. Macdonald and Derek Goodwin of the British Museum (Natural History) have courteously furnished information on a hybrid specimen housed in that institution. In the course of this study, Mr. Francis S. L. Williamson kindly donated to the Museum of Vertebrate Zoology the specimen of Anna x Allen hummingbird described by him earlier (1957). Dr. Joe T. Marshall, Jr., generously permitted us to examine and quote from his field notes. Dr. Seth B. Benson offered several helpful suggestions. Dr. Alden H. Miller has read and criticized the manuscript and has helped in many other ways. We are especially indebted to Mr. Gene M. Christman for preparing the illustrations.

## ACCOUNTS OF HYBRIDS

Comparative material in this study consisted of samples of 20 adult males of each of the parental species from the collection of the Museum of Vertebrate Zoology. Males only were used in the comparisons and in preparation of the following descriptions because all the hybrids were males. These samples, where possible, were chosen to be geographically and seasonally comparable to the hybrids. Weights and measurements are from these samples, with some additions. In the accounts which follow, nomenclature of feather tracts and body regions is that of Aldrich (1956).

Accurate determination of the colors of iridescent hummingbird gorgets and crowns is extremely difficult because these brilliant structural colors vary with each minor change of position of the specimen. The authors are aware that the impressions recorded here may not agree fully with those of other investigators.

*ARCHILOCHUS ALEXANDRI* x *SELASPHORUS PLATYCERCUS*

This specimen was taken by the junior author near the Snyder Ranch, 500 feet elevation, one-half mile west of the Colorado River in extreme southern Clark County, Nevada, on April 1, 1958. The bird, no. 136628 in the Museum of Vertebrate Zoology, is a male (left testis 2.5×1.5 mm.) and weighed 3.8 grams.

The hybrid appears, on the basis of coloration, as if *platycercus* could have been involved in its parentage, but the decisive evidence pointing to this conclusion is the definite emargination of the tip of the trailing edge of each outer remex (see fig. 1). A number of features of the hybrid establish that *A. alexandri*, rather than *C. costae*, is the other parent. The presence of slight notches on the tips of certain primaries (see fig. 1) definitely indicates a member of the genus *Archilochus*. Furthermore, *A. alexandri*, rather than *A. colubri*, is suggested as the probable parent because of the sooty, non-iridescent anterior interramal region of the throat of the hybrid.

## DESCRIPTION

*Capital tract.*—When observed under bright light, the tips of the crown feathers of *S. platycercus* are bright metallic green with some hint of bronze or turquoise depending on the specimen and the direction of the light. The same feathers in *A. alexandri* are much darker green, are duskier, and lack the brilliant sheen of *S. platycercus*. The hybrid definitely tends toward *A. alexandri* in this feature, although the feathers are lighter green than in any example of that species studied. The feathers in the frontal region are shiny green in *S. platycercus*, blackish in *A. alexandri*, and sooty, but with

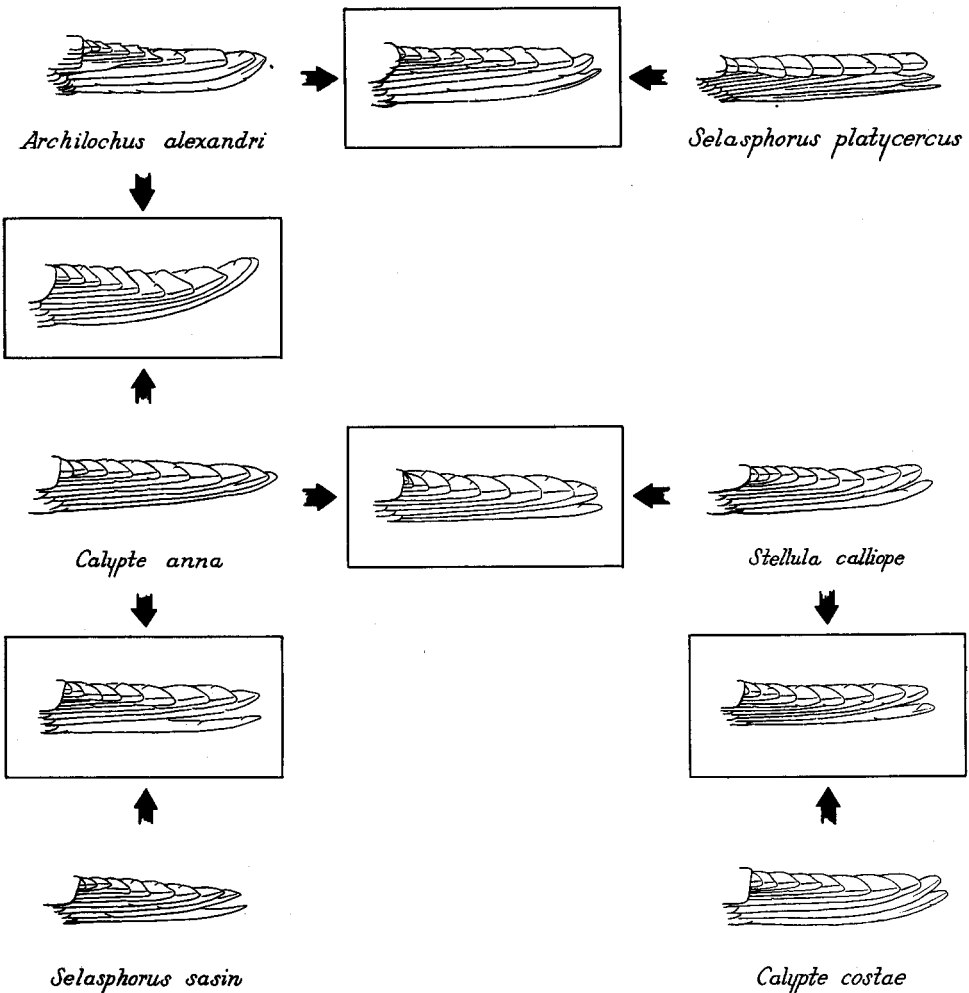


Fig. 1. Left wings of hummingbirds, showing the blending of parental characters in the hybrids. Hybrids are shown between the parental forms.

a faint greenish tinge, in the hybrid. The white postocular spot typical of both parent species is likewise present in the hybrid. In *S. platycercus* the loreal feathers are variably buffy or gray with tiny flecks of green or brown. In *A. alexandri* these feathers are sooty brown or blackish terminally with gray bases. The hybrid is intermediate with an apparent mixture of sooty gray and buffy feathers in the loreal region.

*Spinal tract.*—In *S. platycercus* the feathers of the dorsal surface are similar to those of the crown in that they are brightly iridescent blue- or bronze-green. The same feathers in *A. alexandri*, although more iridescent than those of the crown of that species, are a much duller bronze-green. The hybrid is intermediate in this feature.

*Ventral tract.*—The posterior parts of the malar regions and the auricular regions of *S. platycercus* are characterized by pale buff feathers flecked with brown. These feathers in *A. alexandri* are uniformly blackish. In the hybrid the individual feathers of this region are characterized by having both buffy and sooty brown barbs, with the innova-

tion of green flecking. The iridescent gorgets of both *S. platycercus* and *A. alexandri* are similar in general configuration, except that *S. platycercus* usually has slightly longer "tails" bilaterally. The gorget feathers in *S. platycercus* are broadly tipped with rose red, the basal parts being pale gray. A narrow transverse band of iridescent green occurs between the red and the gray portions of many gorget feathers, particularly those of the "tails." In *A. alexandri* the anterior one-half of the gorget is composed of black-tipped feathers with grayish brown bases. The feathers of the posterior part of the gorget are violet tipped and also have grayish brown bases. Surprisingly, in this species also, a narrow band of iridescent green occurs on these feathers between the violet and the grayish brown portions. The feathers of the anterior one-fourth of the gorget of the hybrid are dark brown (a few are metallic green) edged with buff. The tips of the remaining gorget feathers are lavender (thus intermediate between the rose-red of one parent and the violet of the other) with the bases grayish brown. Iridescent green bands, as found in both parents, are present on the gorget feathers of the hybrid between the lavender tips and the gray-brown feather bases.

The feathers lying immediately posterior to the gorget are grayish white in *S. platycercus* and brownish gray in *A. alexandri*. The hybrid is similar to *S. platycercus* in this respect. In the sternal and abdominal regions of *S. platycercus* the feathers bear median splotches of metallic bronze-green with the barb tips variably gray or rufous. The same feathers in *A. alexandri* have brown and/or dull metallic green median spots, with barb tips of either brown or gray; there is no indication of rufous. None of the rufous evident on the flank feathers of *S. platycercus* is shown by the hybrid. With the exception of the presence of more metallic green and less brown, the hybrid resembles *A. alexandri* more closely than it does *S. platycercus* in coloration of the abdominal feathers.

*Alar tract.*—The marginal coverts of the hybrid are similar in coloration to *A. alexandri* in being dark green with an olive tinge rather than bright iridescent green as in *S. platycercus*. The general coloration of the flight feathers is the same in both the parent species and in the hybrid. In males of *S. platycercus* the outer two primaries (numbers 9 and 10) are peculiarly modified in shape, apparently correlated with the shrill buzzing sound produced by these birds in flight. Male *A. alexandri* possess no such modifications. Figure 1 depicts the wing of each parent species and of the hybrid, which is intermediate in the degree of emargination of the tips of the outer two primaries. The tips of primaries 3 through 8 are more rounded in *S. platycercus* and more pointed in *A. alexandri*. Characteristically, the tips of the inner vanes of primaries 3 through 7 in *A. alexandri* are distinctly notched. The hybrid is intermediate in the shape of the primary tips. The notches are developed on primaries 5 and 6 of the left wing and on primaries 5 and 7 of the right wing, whereas other primaries of the hybrid show only faint indications of notching.

*Caudal tract.*—Viewed from the dorsal aspect, the tails of the parent species are strikingly dissimilar. In *S. platycercus* rectrices 1-1 differ from the outer four pairs by being iridescent blue-green, rather than dark purplish brown; all are edged with rufous or buff. In contrast, the inner two pairs of rectrices (1-1 and 2-2) of *A. alexandri* are dark iridescent green, with pairs 3-3, 4-4, and 5-5 being dark purplish along the feather shafts and bordered with dull green. Rectrices 1-1 of the hybrid are similar in coloration to those of *A. alexandri*. Rectrices 2-2 are uniformly purplish brown with a narrow band of greenish running the length of the outer edge of each feather. Near the bases of these feathers a faint tinge of rufous is apparent, superimposed on the lateral greenish band. The remaining three pairs of rectrices of the hybrid are dark purplish and show only a trace of green along their outer edges, possessing no rufous whatever. With regard to the coloration of the tail the hybrid resembles *A. alexandri* more closely

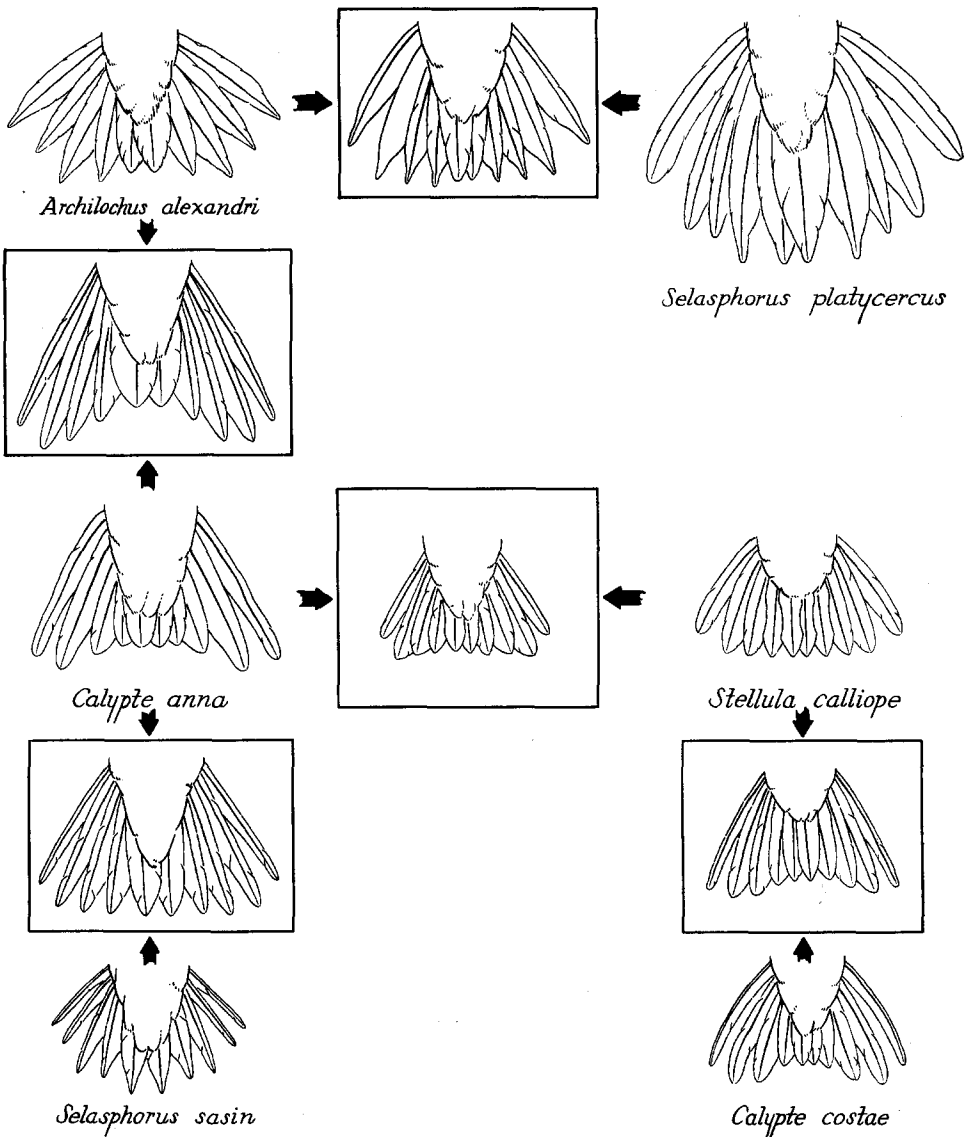


Fig. 2. Dorsal view of hummingbird tails, showing the blending of parental characters in the hybrids. Hybrids are shown between the parental forms.

than it resembles *S. platycercus*, particularly by reason of its virtual lack of rufous edges on the lateral rectrices. Figure 2 illustrates the tails of the parent species and that of the hybrid. Of particular interest in the intermediacy in shape of the tips of rectrices 1-1, 2-2, and 5-5 of the hybrid.

*Mensural characters.*—It can be seen from tables 1 and 2 that in our samples we found no overlap between *A. alexandri* and *S. platycercus* in length of wing, tail, or central rectrix. The hybrid falls between the ranges of the two parent species in these

measurements but is much closer to *S. platycercus* than to *A. alexandri*. In length of culmen and in body weight (tables 1, 3) the parental types are closely similar. In both these features the hybrid is near the upper extremes of the sample ranges.

In summary, the hybrid is intermediate in most characteristics of morphology and color. However, in coloration of the crown, abdomen, tail, and marginal wing coverts

TABLE 1  
MEASUREMENTS IN MILLIMETERS OF CULMEN AND WING OF HYBRID HUMMINGBIRDS  
AND OF PARENTAL SPECIES

	Culmen			Wing		
	N	Mean with standard error	Range	N	Mean with standard error	Range
<i>Selasphorus platycercus</i>	17	17.3±.15	16.4-18.8	18	49.5±.20	48.0-50.9
Hybrid		18.7			47.0	
<i>Archilochus alexandri</i>	17	17.5±.17	16.1-18.6	20	41.9±.16	40.7-43.2
Hybrid		.....			46.3	
<i>Calypte anna</i>	20	17.4±.14	16.1-18.4	20	49.1±.19	47.8-51.2
Hybrid		16.1			44.7	
<i>Stellula calliope</i>	19	13.7±.11	13.1-14.7	19	38.9±.15	38.0-40.0
Hybrid		15.2			42.8	
<i>Calypte costae</i>	18	16.6±.13	15.7-17.7	20	44.2±.17	43.0-45.4

the specimen more closely resembles *A. alexandri*. A preponderance of *S. platycercus* features appears in the coloration of the ventral cervical region and in length of wing and tail.

#### DISCUSSION

The hybrid was shot from its perch on a dead twig in the top of a honey-mesquite tree (*Prosopis juliflora*) growing at the ecotone between the riparian vegetation of large Fremont cottonwoods (*Populus fremontii*), tree willows (*Salix*), mesquite, and arrowweed (*Pluchea*) on the river floodplain and the vegetation dominated by creosote-bush (*Larrea*) on the first river terrace. The Black-chinned Hummingbird is resident in the local riparian growth (Linsdale, 1936:66; N. K. Johnson, MS), whereas the Broad-tailed Hummingbird does not occur as a resident species in the area where the hybrid was taken. The nearest known breeding locality of the latter species is Clark Mountain, Providence Mountains, San Bernardino County, California, located approximately 60 airline miles to the northwest (Johnson, Bryant, and Miller, 1948:294). This points to the probability that the hybrid was in migration at the time of collection. We can postulate the point of origin of this hybrid as being somewhere in the vast area of known geographic sympatry of *A. alexandri* and *S. platycercus* lying to the north of the collection locality in the Great Basin-Rocky Mountains region. The Broad-tailed Hummingbird inhabits deciduous thickets growing along streams, willow copses in meadows, and various mixed growths of piñon, juniper, mahogany, and aspen on slopes in mountainous country. The Black-chinned Hummingbird occurs in several habitats, depending upon the locality, from deciduous growth in cultivated valleys to canyon streamside shrubbery and mixed woodland vegetation at higher elevations on mountainsides. The authors are aware of no explicit report of these two hummingbird species occurring together under conditions of local ecologic sympatry, although this situation is implied

TABLE 2  
MEASUREMENTS OF TAIL (LONGEST RECTRICES) AND CENTRAL RECTRICES  
OF HYBRID HUMMINGBIRDS AND PARENTAL SPECIES

	Tail			Central rectrices		
	N	Mean with standard error	Range	N	Mean with standard error	Range
<i>Selasphorus platycercus</i>	18	33.7±.21	32.8-35.4	18	32.1±.25	29.4-33.6
Hybrid		30.9			28.6	
<i>Archilochus alexandri</i>	20	25.6±.16	24.6-27.1	20	22.4±.19	21.1-24.3
Hybrid		30.3			24.1	
<i>Calypte anna</i>	20	31.6±.19	30.1-33.3	20	25.0±.15	23.7-26.1
Hybrid		28.4			22.1	
<i>Stellula calliope</i>	20	21.2±.12	20.4-22.0	20	18.8±.12	17.9-20.1
Hybrid		23.2			19.8	
<i>Calypte costae</i>	20	23.0±.22	21.0-24.4	20	19.3±.15	18.1-20.6

for Utah (see beyond). The distribution of the two species in Nevada and Idaho are too poorly known to permit detailed discussion, but in Utah their altitudinal ranges overlap in several places. According to Behle (1943:41) in southwestern Utah *A. alexandri* "was not found above 6000 feet, but it did occur in the pygmy forest. It has been found ranging up as high as 9000 feet in the Wasatch Mountains east of Salt Lake City [north-central Utah]." Concerning *S. platycercus*, Behle continues (*op. cit.*:42): "this form is wide ranging like the black-chinned species, being commonly encountered from the lowlands up to the high mountain meadows around 9000 feet." In their report on the birds of the Kanab area, Behle, Bushman, and Greenhalgh (1958:14-15) indicate considerable habitat overlap between the two species. Specifically, in a table where the

TABLE 3  
WEIGHTS IN GRAMS OF HYBRID HUMMINGBIRDS AND OF THE PARENTAL FORMS

	N	Mean with standard error	Range
<i>Selasphorus platycercus</i>	17	3.3±.11	2.5-4.1
Hybrid		3.8	
<i>Archilochus alexandri</i>	16	3.1±.09	2.7-4.1
<i>Calypte anna</i>	16	4.3±.17	3.3-5.8
Hybrid		3.0	
<i>Stellula calliope</i>	24	2.5±.06	1.9-3.2

birds are arranged according to their ecological occurrence during the breeding season, they list both *A. alexandri* and *S. platycercus* as inhabiting "submontane shrub," "montane riparian woodland," and "mountain meadow and parkland." At Bryce Canyon the Black-chinned Hummingbird is further stated to be "a common summer resident along the rim and in canyons around 8000 feet and below," indicating high mountain occurrence for the species in that region. Ecologic details concerning the two species in other parts of the northern Rocky Mountains have apparently not been published. It must

be emphasized that the few areas of possible hybridization mentioned here merely represent places where the two hummingbird species have been known to occur in close proximity and north of where our hybrid was taken. Considerable field work will be necessary to elucidate the ecologic relationship between *A. alexandri* and *S. platycercus* where they are sympatric.

#### CALYPTE ANNA x ARCHILOCHUS ALEXANDRI

This cross is known from a single specimen described as *Trochilus* (or *Archilochus*) *violajugulum* by Jeffries (1888). The male specimen is no. 40932 in the Museum of Comparative Zoology. It was collected at Santa Barbara, California, on April 5, 1883.

The identity of this specimen was disputed by Peters (1945), who felt that the cross involved *C. costae* rather than *C. anna*. We have examined the hybrid carefully with this in mind and feel that we can definitely eliminate *C. costae* from consideration for several reasons. In length of wing, tail, and middle rectrix, the bird is larger than either *A. alexandri* or *C. costae*, but it is nearly exactly intermediate between *C. anna* and *A. alexandri*. *Calypte costae* possesses an extremely narrow outer rectrix; this feather is equally wide in *C. anna*, *A. alexandri*, and the hybrid bird. The gorget is crescent-shaped in *C. costae*, the lower throat being white. In the hybrid the gorget is as extensive as in *C. anna*, where it covers the entire throat. Further, the gorget shows a definite reddish cast which could have come from *C. anna* but not from *C. costae*. The feathers of the lateral extensions of the gorget are narrow in *C. costae*; these same feathers are wide and more rounded in both *C. anna* and the hybrid.

Ecologically, a mating between Anna and Black-chinned hummingbirds is more likely than a Costa x Black-chinned hummingbird cross. The preferred habitats of *C. anna* and *A. alexandri* are more similar than are those of *C. costae* and *A. alexandri* (Grinnell and Miller, 1944:217-220).

That the parentage of the hybrid involves *Archilochus* is established by the presence of slight notches on the inner vanes of primaries 3, 4, and 5. These notches are characteristic only of *Archilochus* among North American hummingbird genera (Ridgway, 1892). Although the eastern Ruby-throated Hummingbird (*Archilochus colubris*) must be considered, it can almost certainly be ruled out for geographic reasons. Because the other parent seems to be *Calypte anna*, *A. colubris* is further eliminated by the obvious influence of "blue" in the hybrid's gorget. Also, the hybrid's chin lacks iridescent feathers, a fact which points definitely to *A. alexandri*.

Jeffries (*op. cit.*) considered the Lucifer Hummingbird (*Calothorax lucifer*) as a possible parent of this bird but discarded the thought on the basis of unspecified differences in the wing and tail.

#### DESCRIPTION

*Capital tract.*—In *A. alexandri* the anterior part of the frontal region consists of dusky feathers, blending posteriorly into the iridescent green, dusky tipped feathers of the coronal region. In *C. anna* the feathers of the frontal and coronal regions are metallic reddish purple, forming a cap bounded posteriorly by the green occipital feathers. The hybrid resembles *A. alexandri* in having a dusky rather than an iridescent crown. The occipital regions of both *A. alexandri* and the hybrid are darker, more dusky, than that of *C. anna*. This is the only hybrid involving a member of the genus *Calypte* in which the color of the crown is not metallic.

*Spinal tract.*—Although both *A. alexandri* and *C. anna* have backs which may be characterized as metallic green, the back of *C. anna* appears rather more golden, that of *A. alexandri* more bronzy. This effect is partly the result of bluish tips on some of the



back feathers of *A. alexandri*, although the basic color of these feathers is also somewhat darker than in *C. anna*. The hybrid is almost exactly intermediate between the two presumed parent species.

*Ventral tract.*—The interramal, malar, and auricular regions of the Black-chinned Hummingbird are black, only the submalar feathers showing the iridescence typical of male hummingbird gorgets. In *A. alexandri*, these latter feathers are dark blue. The lateral feathers of the gorget do not extend into "tails" as they do in *C. anna*. In the latter species the entire gorget, including interramal, malar, and submalar regions, is brilliant iridescent rose-red. In the hybrid, the interramal and malar feathers are black, although this non-iridescent area is not as extensive as in *A. alexandri*. The rest of the gorget is "violet with a tendency to steel blue at the feather tips," as described by Jeffries (1888). The hybrid possesses short lateral extensions or "tails" to the gorget.

Posteriorly the gorget of *A. alexandri* is bounded by a white or light gray band, whereas this lower throat region of *C. anna* is tinged with grayish green. The hybrid has a light gray band in that region. The breast and belly of *C. anna* are dark, the many bronze-green feathers being edged with gray. In *A. alexandri* there are fewer metallic green feathers on the undersurface, the whole appearing lighter, more gray and less green, than in *C. anna*. The extent of the green is less in *A. alexandri*, the belly area being whitish. The hybrid resembles *C. anna* in the extent of green on the undersurface, but it is lighter below in overall appearance, being intermediate between the supposed parental forms.

The undertail coverts of *C. anna* are dark, with occasional bronze-green feathers edged with gray. In *A. alexandri* the feather centers are lighter and the edging tends more toward white. The hybrid manifests the intermediate condition of dark, bronzy centers and broad whitish edgings.

*Caudal tract.*—The outer four rectrices of *A. alexandri* are very attenuated, the narrowing affecting especially the inner vanes. These feathers in *C. anna* are wide to the tips, which are rounded rather than pointed. In the hybrid these four lateral rectrices taper to narrow rounded points, a condition combining the features of the parental forms. This intermediacy is especially apparent on the outermost rectrices (fig. 2). The central or deck rectrices are rounded in both *C. anna* and *A. alexandri*, but they are relatively more tapered in the latter. Again, the hybrid is intermediate (fig. 2). In relative length of the rectrices the hybrid resembles *C. anna*, the tail being forked rather than notched as in *A. alexandri*.

The inner rectrices of the hybrid are bronze-green, appearing somewhat more metallic than those of either of the presumed parents. The other rectrices are dark purplish green in both *A. alexandri* and *C. anna*, although the latter has a light edging to the inner vanes of the outer two rectrices. The rectrices of the hybrid are similarly colored but lack the light edgings.

*Alar tract.*—The outer primary of *A. alexandri* is wider than that of *C. anna* (4 mm. versus 3 mm.). The outer vane of this feather is wide in *A. alexandri* but very narrow in *C. anna*. The hybrid is like the Black-chinned Hummingbird in both of these characters (fig. 1) as well as in characters of primaries 9, 8, and 7.

Ridgway (1892:326) characterized the inner six primaries of birds of the genus *Archilochus* (then *Trochilus*) as "abruptly and conspicuously smaller than the rest, with their inner web more or less notched and toothed at the tip (except in *T. violajugulum*)." Writing further of this peculiarity of *T. violajugulum*, Ridgway (*op. cit.*) states: "there is an indication of the tooth-like projection just anterior to the end of the web." There is in *Calypte anna* neither a notch on the inner primaries nor a noticeable size reduction of these feathers. The inner six primaries of the hybrid (*violajugulum*)

are more similar, in both relative size and in shape, to those of *C. anna* than to those of *A. alexandri*.

*Mensural characters.*—*Calypte anna* is considerably larger than *A. alexandri*, especially in wing length, there being no overlap between the species (table 1). The hybrid is intermediate in this measurement, but it is slightly nearer the larger parent. The tail of the hybrid is near that of *C. anna* in shape, as reflected by the relative lengths of the longest and central rectrices (table 2). The hybrid is nearer *C. anna* in actual, as well as relative, length of these feathers. Unfortunately, the culmen of the hybrid is broken and there is no weight recorded. The parents are virtually identical in culmen length, however, and the overall size of the hybrid suggests that it would tend toward *C. anna* in weight.

#### DISCUSSION

The geographic ranges of the Black-chinned and Anna hummingbirds overlap broadly in coastal southern California, north to Santa Clara County, and in the foothills bordering the central valley of California. Both species are mainly residents of the Upper Sonoran Life-zone (Grinnell and Miller, 1944). Although their preferred habitats are different, the oak woodland formation is second in importance for both species (Miller, 1951). This indicates that opportunities for these birds to interbreed are many.

Consideration of the normal breeding seasons of the two forms, however, indicates otherwise. The resident Anna Hummingbird is a very early breeder. Woods (*in Bent*, 1940:372) writes: "The nesting season begins before the arrival of any of the migrants, sets of eggs having been found . . . as early as December. The nesting probably continues normally through late winter and spring and sporadically throughout summer." In a study of hummingbird breeding seasons in the Santa Barbara area, Pitelka (1951*a*) showed that over three-fourths of the Anna Hummingbird nest records were earlier than the first nesting record of the Black-chinned Hummingbird. But because of the long breeding period of *C. anna*, the nesting seasons of the two species overlapped from mid-April to the end of June.

Since the presumed hybrid between these species was taken at a time when one of the parental forms is in migration, it is possible that the hybrid itself was a migrant. The location of collection does not, therefore, necessarily indicate the place of origin of the bird. Because the collection locality is coastal, however, a coastal origin rather than one in the central valley may be postulated. Operating under the assumption that hybridization is most likely where one or both of the parental forms is rare, it seems possible that this bird originated in the coastal area between Santa Clara and Santa Barbara counties, California, in the northern part of the range of *A. alexandri*.

#### CALYPTE COSTAE X ARCHILOCHUS ALEXANDRI

Thayer and Bangs (1907) include this cross in a list of hybrid hummingbirds then known from California. These authors are cited by Taylor (1909), Simon (1910), Berlioz (1929), Cockrum (1952), and Gray (1958), but none of these works gives a reference to a prior mention of this cross.

In 1888 Jeffries had described *Trochilus violajugulum* and was aware that his specimen might be a hybrid of the Anna and Black-chinned hummingbirds. One can assume that Jeffries would have remarked on a *C. costae* x *A. alexandri* hybrid, if he had known of one. Thayer and Bangs (*op. cit.*) did not merely substitute the name of *C. costae* for *C. anna*; they list both as having hybridized with *A. alexandri*.

A thorough search of American ornithological journals and of the Zoological Record for the years between 1888 and 1907 has failed to reveal a mention of a hybrid involving the Costa and Black-chinned hummingbirds. Although Thayer's collection is in the

Museum of Comparative Zoology, there is no bird designated *C. costae* x *A. alexandri* present there (Greenway, *in litt.*). Peters (1945) re-examined Jeffries' *Trochilus violajugulum* and thought that it represented *C. costae* x *A. alexandri* rather than *C. anna* x *A. alexandri*, but he gave no reasons for this choice. We have examined this specimen, and as noted earlier agree with earlier workers, not with Peters.

Unless further information is forthcoming, it appears that *Calypte costae* x *Archilochus alexandri* should be deleted from any list of North American hybrid hummingbirds.

#### CALYPTE COSTAE x STELLULA CALLIOPE

This hybrid was first recorded by Hartert (1900), in whose report little information is given except that the specimen was "obtained by Mr. O. T. Baron in California." This cross was not listed in the compilations of Thayer and Bangs (1907), Taylor (1909), or Simon (1910), and is not mentioned by Ridgway (1911). The same bird was reported a second time (Rothschild, 1927), as follows: "Lord Rothschild exhibited two Humming-birds which have hitherto been considered as hybrids, together with the supposed parent species. . . . the one bird was an undoubted hybrid between *Stellula calliope* (Gould) x *Calypte costae* (Bourc)." Both reports of this hybrid escaped Berlioz (1929) and Cockrum (1952), although they are listed by Gray (1958).

The bird is now no. 484693 in the American Museum of Natural History. The label gives no collecting date or locality. The sex is not given, but we assume from the plumage that the bird is a male.

The influence of *Calypte* in this cross is indicated by the iridescent crown. That *Calypte costae* was involved rather than *C. anna* is suggested by the narrowness of the outer rectrix. That the hybridization involved *Stellula calliope* is indicated by the presence of rufous on the tail, the square tips on primaries 5, 6, and 7, and white bases on the gorget feathers.

#### DESCRIPTION

*Capital tract.*—The entire crown of the Calliope Hummingbird is green, except for white lores, whereas the Costa Hummingbird has a cap of iridescent blue-violet feathers covering all but the postocular, superciliary, and occipital regions. The crown of the presumed hybrid has iridescent purple feathers on the loreal, frontal and part of the coronal regions, extending slightly posterior to a line connecting the eyes. There are two feathers with iridescent tips on each side of the hybrid's head, roughly at the juncture of the coronal, occipital, and superciliary regions. The rest of the coronal region, as well as the occipital and superciliary regions, is bronze-green, resembling *S. calliope*. There is a white postocular mark in the hybrid, as in both parental forms.

*Spinal tract.*—The entire back of the hybrid is metallic green, more golden than bronzy, but much nearer *S. calliope* than *C. costae*.

*Ventral tract.*—The gorget of *C. costae* includes feathers of the interramal and malar regions, the latter feathers extending in long lateral "tails." The gorget is brilliant purple or blue-violet. The feathers of the center of the gorget are buffy at their bases, whereas the elongated malar feathers are green for the proximal two-thirds of their length. The gorget is definitely crescent-shaped, the central portion terminated sharply by a white or light gray band which extends posteriorly over the throat and laterally beneath the "tails" onto the sides of the neck.

In *S. calliope*, feathers of the malar region are white, and the iridescent purplish red gorget feathers arise mainly from the interramal region. The lateral "tails" are very narrow elongated feathers of the sides of the submalar region. The spotty effect in the gorget of *S. calliope* is a result of the fact that the feathers of the interramal region are

modified for iridescence only on their tips and that the white feather bases are partly exposed. The feathers of the gorget "tails" are iridescent only for the distal one-half or one-third of their length, and the white bases of these feathers also show through, or actually around, the narrow colored ends. The gorget is bounded posteriorly by a white throat band which extends laterally beneath the gorget "tails" onto the sides of the neck as in *C. costae*.

The gorget of the hybrid is iridescent purple or lavender. It includes the feathers of the interramal and malar regions. Medially, the extent of the iridescent modification of these feathers is similar to that of *C. costae*, permitting only a little of the white feather bases to show. The lateral feathers are iridescent for about the terminal one-third of their length. Proximal to this tip, there is a narrow green band; the feather bases are white and show through. The feathers of the gorget "tails" are wider than in *S. calliope* but not as wide as in *C. costae*. The throat band of the hybrid is white and extends onto the sides of the neck as in both parents.

The remainder of the undersurface of the hybrid is solidly colored, as in *C. costae*, but of a lighter, more golden green than the bronze green of that species. There is only a faint indication of the midventral white stripe of *S. calliope*. The undertail coverts are largely white, as in *S. calliope*; the most proximal coverts have metallic green centers, a condition only occasionally found in *S. calliope* but present to a high degree in *C. costae*, where the entire crissum has a greenish tint.

*Caudal tract.*—In *C. costae* the outer (5th) rectrices are very narrow, and rectrix width increases toward the broad central pair. All the rectrices are rounded. In *S. calliope* the bluntly pointed subspatulate rectrices are all of approximately the same width, about equalling the third pair of *C. costae*. The intermediate width of the hybrid's rectrices is most evident in the first and fifth pairs (fig. 2). The shape of the tips of the rectrices is also intermediate.

The proximal halves of both vanes of rectrices 1-1 and the same portion of the outer vanes of rectrices 2-2, 3-3, and 4-4 of *S. calliope* are edged with rufous, a color which is completely absent in the tail of *C. costae*. The outer vanes of the hybrid's rectrices 1-1 and 2-2 are edged to the same extent with cinnamon buff. The tail of *C. costae* is green, with occasional hints of blue, whereas *S. calliope* has a tail of purplish black "broadly tipped with dull brownish gray" (Ridgway, 1911). In the hybrid the rectrices are purplish green, broadly tipped with lighter green.

*Alar tract.*—The central primaries of the hybrid are similar to those of *S. calliope* in being more bluntly rounded, the tips of some primaries (especially 5, 6, and 7) being nearly square. In *C. costae* the tapered parts of the inner vanes of the central primaries are longer, imparting a more pointed appearance to these feathers. The color of the wing is very similar in both the presumed parent species and the hybrid.

*Mensural characters.*—The Costa Hummingbird exceeds the Calliope Hummingbird in length of both culmen and wing, there being no overlap between the two species (table 1). In both these measurements the hybrid falls into the intermediate zone. *Stel-lula calliope* is only slightly smaller than *C. costae* in length of the tail and central rectrices (table 2). The hybrid slightly exceeds the mean of the larger parent in both these features. No comparison of weight is possible.

#### DISCUSSION

Without knowledge of where or when the bird was taken, other than "California" (Hartert, 1900), it is difficult to say much concerning the origin of this hybrid. *Calypte costae* is in general a bird of "deserts or desert-like washes, mesas or side-hills" (Grinnell and Miller, 1944), and it is found in the Lower and Upper Sonoran life-zones

(Miller, 1951). The Calliope Hummingbird, on the other hand, is a montane species, nesting from 4000 to 9000 feet elevation in California (Grinnell and Miller, *op. cit.*) in the Transition and Canadian life-zones (Miller, 1951). Thus, even where the geographic ranges of the two species overlap, they are normally separated altitudinally.

One region of possible contact is in the Toyabe Mountains of central Nevada (Linsdale, 1938), where a single Costa Hummingbird was seen in June at 7100 feet elevation, and where Calliope Hummingbirds were "present in only limited numbers" at 7000 feet elevation. There may be similar situations in other Great Basin mountain ranges. Grinnell (1928) reported both species from the Sierra San Pedro Mártir of northern Baja California, where individuals of *C. costae* (p. 132) "occur high on the mountains in summer, even to 8500 feet altitude."

#### CALYPTE ANNA X STELLULA CALLIOPE

The single bird presumed to be a result of a mating of the Anna and Black-chinned hummingbirds was mentioned by Grinnell (1928) and was briefly described by Berlioz (1930). The adult male bird, no. 47983 in the Museum of Vertebrate Zoology, was collected by Chester C. Lamb near Vallecitos, 7500 feet elevation, Sierra San Pedro Mártir, Baja California, México, on June 19, 1926. It weighed 3.0 grams.

The influence of *S. calliope* in this hybrid is indicated by the white bases and the narrowness of the feathers of the lateral gorget extensions. The coronal iridescence is indicative of at least partial *Calypte* parentage, whereas the color of the crown patch and gorget and the width of the outer rectrices indicate that *C. anna* rather than *C. costae* was involved.

#### DESCRIPTION

*Capital tract.*—The frontal, superciliary, and coronal regions of *S. calliope* are bronze green; the loreal region is white. In *C. anna* these four regions of the head are covered with iridescent rose-red feathers. In the hybrid iridescent lilac feathers are largely restricted to the frontal region, a few occurring among the green superciliary and coronal feathers. The loreal region of the hybrid has both white and iridescent feathers. The coronal regions of the hybrid and of *S. calliope* are similar, and both agree with *C. anna* in the color of the occipital region. The iridescent feathers of the hybrid are like those of *C. anna* in having the iridescent tips bounded proximally by narrow green bands. The bases of these feathers are gray.

*Spinal tract.*—The back of *C. anna* is darker, more bronzy, than that of *S. calliope*. The dorsal coloration of the hybrid is very similar to *C. anna*.

*Ventral tract.*—The gorget of *C. anna* covers the interramal, malar, and submalar regions, extending posteriorly into lateral "tails" of broad feathers. The proximal two-thirds of these long lateral feathers is greenish gray. The brilliant gorget feathers of *S. calliope* arise mainly from the interramal region; the proximal halves of the lateral "tail" feathers are white, and these feathers are narrow. The gorget of the hybrid is restricted to the interramal and submalar regions, the malar region being more greenish than in *S. calliope*, with a few iridescent feathers. The white feather bases responsible for the spotty effect of the gorget of *S. calliope* replace, in the hybrid, the gray bases of *C. anna*, but they are less extensive and thus are seen as only a few small spots. The feathers of the hybrid's gorget "tails" are of intermediate width and are less pointed than those of *S. calliope*. The bases of these feathers are white and the iridescent tips are bounded proximally by a faint green band.

The gorget of this hybrid was described by Berlioz (1930) as "brightly shining rosy-purple," with "lilac reflections." We agree with this description, which points to the intermediacy between the two presumed parental species. The hybrid is also intermediate

in respect to the color of the throat band, which is greenish gray in *C. anna*, white in *S. calliope*, and very light greenish white in the hybrid.

The remainder of the underparts of *C. anna* is dark gray; metallic green feathers are prominent on the sides of the breast and abdomen. The hybrid resembles the coloration of *C. anna* in these areas, but it is much lighter; there is no indication of the midventral white stripe of *S. calliope*.

The undertail coverts of *C. anna* are green with broad gray margins; those of *S. calliope* are nearly pure white. In the hybrid these feathers are white with narrow, light green centers.

*Caudal tract.*—The inner three pairs of rectrices in *C. anna* are broad in comparison to the lateral pairs (approximately 8 mm. versus 3 mm.). As has previously been stated, the Calliope Hummingbird's rectrices are all similar in width (3 to 4 mm.), and the central two pairs are subspatulate and pointed. All the tail feathers of *C. anna* and the lateral three pairs of rectrices of *S. calliope* are rounded. In the matter of relative width of rectrices the hybrid is intermediate (outer rectrix 3.3 mm., central rectrix 5.5 mm. wide). Intermediacy in the shape of the rectrix tips and of the tail as a whole is shown in figure 2.

The central rectrices (1-1) of *C. anna* are bronze green, pair 2-2 is purplish green, and the lateral pairs are purplish black. On most specimens of *C. anna* rufous is completely absent from the tail, although Williamson (1957:122) found this color on a small number of adult males. The Calliope Hummingbird has rufous edging on the central pairs of rectrices, which are otherwise purplish black with gray brown ends. The hybrid has rufous edges on the inner vanes of rectrices 4-4 and 3-3 and on both vanes of 2-2 and 1-1. The feathers are otherwise entirely purplish black.

*Alar tract.*—The difference between the primaries of *C. anna* and *S. calliope* are the same as those between *C. costae* and *S. calliope* (p. 14). On the present hybrid the blunt tips of primaries 5, 6, 7, and 8 show much influence of the Calliope Hummingbird (fig. 1). Wing color is similar on the hybrid and both parental species.

*Mensural characters.*—As seen from tables 1, 2, and 3, *C. anna* is a "giant" hummingbird when compared to *S. calliope*. There is no overlap between the species in any measurement we made, and in length of both wing and tail the Calliope Hummingbird is smaller by over 30 per cent. The wing length of the hybrid is intermediate between the two parents. In all other measurements the bird tends toward the size of *C. anna*. The weight of the hybrid is within the range of variation of our sample of *C. anna* but is nearest the mean weight of the Calliope Hummingbird.

#### DISCUSSION

That hummingbirds of the extremes in size represented by *C. anna* and *S. calliope* should interbreed seems extremely unlikely, and Berlioz (1930) has remarked that this "difference of size may render rather abnormal such an occurrence." A seemingly more difficult barrier to overcome is the almost complete geographic and altitudinal separation of the species. The Anna Hummingbird is a species of Upper Sonoran chaparral or oak woodland, while the Calliope Hummingbird prefers montane and subalpine forest in the Transition and Canadian zones (Miller, 1951). Even where both species occur in the same geographic localities they seem to be isolated altitudinally (see, for example, Grinnell, 1908). Also the statement by Berlioz (*op. cit.*) that "both species may occur together at breeding time in the mountains of California" seems incorrect.

Even in the Sierra San Pedro Mártir, where the specimen under consideration was collected in late June, the breeding ranges of the presumed parents are separated by several thousand feet of elevation. These differences in preferred habitat and life-zone

suggest that one or both of the parents was a vagrant, well out of its normal environment, and make it impossible to postulate with confidence the point of origin of this hybrid.

#### CALYPTE COSTAE x SELASPHORUS PLATYCERCUS

A male bird presumed to be of this parentage was reported and described by Huey (1944). The specimen was collected on June 21, 1932, in the conifer belt in the Rincon Mountains of Pima County, Arizona. The present location of this bird is unknown; it cannot be found at the San Diego Museum of Natural History (Huey, *in litt.* to Alden H. Miller, Aug. 13, 1959).

The following description of this hybrid is condensed from Huey (1944). The purplish red gorget combines the colors of the parental forms, and these feathers are intermediate in shape. The crown is speckled, some feathers green as in *S. platycercus*, others purplish red, reminiscent of *C. costae*. The ventral surface of the second rectrix is colored like that of *S. platycercus* distally, but it is like that of *C. costae* basally. The form of the tail and wing is intermediate between the parents. In size, the hybrid tends toward the larger *S. platycercus*.

Because the parental forms breed in adjacent life zones in the Rincon Mountains, Huey assumed that the hybrid had been produced by parents living at the borders of their preferred habitats.

#### SELASPHORUS RUFUS x STELLULA CALLIOPE

A male bird considered to be of this origin was described by Thayer and Bangs (1907). Although the specimen was once in Thayer's collection, its present location is unknown. In its place at the Museum of Comparative Zoology is a label—probably not the original—reading "Oakland [California], May 8, 1896, Locust Blossoms" (Greenway, *in litt.*).

Thayer and Bangs (*op. cit.*) stated that the specimen was "somewhat intermediate between adult males" of the parent species, and they described it as follows:

"The back is green, duller and more coppery than in *Atthis* [now *Stellula*] *calliope*, the upper tail coverts and rectrices are edged with rufous, the rufous edging reaching nearly to the tips of the feathers on the inner webs of the rectrices and about to the middle on the outer webs; the cheeks, sides of the body and under tail coverts are all clouded with rufous; the gorget, composed of feathers more pointed and narrower than in *Selasphorus rufus*, with the white bases showing slightly through, is of the most gorgeous ruby red, different from either *Selasphorus rufus* or *Atthis calliope*; the shape of the rectrices corresponds rather better with male examples of *Selasphorus rufus*, the outer rectrices being narrower and pointed, but the tail is short and more nearly square as in *Atthis calliope*."

#### SELASPHORUS RUFUS x CALYPTE ANNA

References to a bird of this parentage seem to have no basis in fact. The cross is listed, but not discussed, by Cockrum (1952) and by Gray (1958). It appears that all references to hybridization involving these species result from disagreement concerning the parentage of *Selasphorus floresii* Gould.

In discussing *S. floresii* (as *Trochilus floresii*) in 1887, Ridgway (p. 315, footnote) states: "This is possibly a hybrid between *T. anna* and *T. rufus*." In 1892 Ridgway compared *S. floresii* to *Calypte anna*, but did not discuss the possibility of hybrid origin. Later Ridgway (1909) again refers to *S. floresii*: "There is not the slightest doubt in my mind that this bird is a hybrid of *Selasphorus rufus* or *S. alleni* [now *S. sasin*] and *Calypte anna* . . ." By 1911 Ridgway's opinion was more definite, but still wavering.

Two conflicting statements appear, as follows (p. 596, footnote): "... *S. floresii* Gould, is undoubtedly a hybrid of *Selasphorus rufus* (or *S. alleni*) and *Calypte anna*"; (p. 616, footnote) "Almost certainly a hybrid of *S. alleni* and *Calypte anna*."

While Ridgway was still undecided, Simon (1910) referred to *S. floresii* as a hybrid between *Selasphorus rufus* and *Calypte anna*. Berlioz (1929) mentions *S. floresii* as representing *C. anna* x *S. rufus* or *S. alleni*. We have been unable to find a description of a hybrid *Calypte anna* x *Selasphorus rufus* except in the context of *S. floresii*. Apparently these are the reports echoed by Cockrum (1952) and Gray (1958).

#### CALYPTE ANNA x SELASPHORUS SASIN

Five male specimens believed to be of this parentage have been reported, including the description of a specimen of this cross as the distinct species *Selasphorus floresii* by Gould (1861). These are:

Hybrid A, Williamson (1957). Woolsey Canyon, Alameda County, California. Collected by Jerry C. Russell on May 20, 1955. Specimen now in the Museum of Vertebrate Zoology, no. 140103.

Hybrid B, Taylor (1909). Nicasio, Marin County, California. Collected by Walter P. Taylor on February 26, 1909. Specimen now in the Museum of Vertebrate Zoology, no. 7125.

Hybrid C, Emerson (1901). Hayward, Alameda County, California. Collected by W. O. Emerson on February 20, 1901. Specimen now in the California Academy of Sciences, no. 46038.

Hybrid D, Bryant (1886). Near San Francisco, California. May, 1885. Specimen formerly at the California Academy of Sciences; believed destroyed by fire in 1906 (Dr. Robert T. Orr, *in litt.*).

Hybrid E, Gould (1861). Locality originally given as Bolaños, Oaxaca, México, but should be Bolaños, Jalisco (Ridgway, 1909:440). The specimen was collected by Flores on an unknown date, probably in California (see Williamson, 1957:120). "There is nothing on the original label except the identity and the words 'Loddiges Collection'" (J. D. Macdonald, *in litt.*). Specimen now in the British Museum (Natural History), no. 1933.11:14:1.

With the exception of the type of "*S. floresii*," we have examined all extant specimens representing hybridization between *C. anna* and *S. sasin*. Williamson (*op. cit.*) described his specimen and both of the parent species in some detail and also commented briefly on the information published by Emerson (*op. cit.*) and Taylor (*op. cit.*), but the specimens collected by the latter two workers have never been thoroughly described. Williamson's bird was originally preserved in both alcohol and Bouin's solution, but it has now been dried and allowed to mummify. Because the colors may have been altered by these chemicals, only mensural data have been taken from this bird. In the account to follow, Taylor's bird (Hybrid B) and Emerson's specimen (Hybrid C) will be compared in detail to Williamson's description of his specimen (Hybrid A) and, where possible, with Hybrid A itself. At our request, J. D. Macdonald and Derek Goodwin have examined Hybrid E in the British Museum (Natural History) and have sent descriptive notes which are appended.

#### DESCRIPTION

*Capital tract.*—Hybrids B and C are similar to Hybrid A in that the reddish iridescence of the crown is confined chiefly to the feathers of the frontal region, rather than also involving feathers of the anterior coronal region as in *C. anna*. However, the tips of these feathers are not "intense red," as stated by Williamson for Hybrid A, but appear purplish red. Furthermore, in hybrids B and C, they do not assume a rufous tinge at



the base of the bill as in Hybrid A. Hybrid B shows a speckling of rufous-tipped feathers in the loreal, superciliary, and auricular regions, but to a lesser extent than does Hybrid A. Hybrid C shows even fewer of these rufous-tipped feathers, which are characteristic of *S. sasin*, and instead emphasizes the gray feathers typical of *C. anna* for these regions. The white postocular spots present in both parent species are found in all three of the hybrids.

*Spinal tract.*—Williamson did not discuss the feathers of this tract. In *S. sasin* the feathers of the dorsal cervical region and of the anterior dorsal region are gray basally and bright metallic green distally; only the tips of the barbs are rufous. In contrast, the feathers of the posterior dorsal region (rump) are entirely rufous. The feathers of *Calypte anna* are similar in coloration throughout the spinal tract, being gray basally and metallic green distally, except for gray-tipped barbs. The shade of green seems to be the same in the two species, but the presence of gray-tipped barbs instead of rufous-tipped barbs on the spinal-tract feathers of *C. anna* gives the dorsal surface of that species a somewhat darker appearance than in *S. sasin*. The present condition of Hybrid A makes color description of it inadvisable. The feathers of the spinal tract of Hybrid B have barbs tipped with both gray and rufous, with the latter color slightly more prominent on barb tips in the posterior dorsal region. There is no indication whatsoever of extensive rufous coloration of any entire feathers in the rump region. Hybrid C is similar except that it possesses mostly gray barb-tips, with rufous coloration barely indicated.

*Ventral tract.*—*Calypte anna* and *Selasphorus sasin* have gorgets similar in configuration, the chief difference being that in the former species the feathers composing the "tails" average greater in length. Hybrids A, B, and C are intermediate in this respect. With regard to coloration of the gorget, Hybrid A was described as being similar to *C. anna* but with a rufous tinge like that of *S. sasin*. This description also loosely fits Hybrid C, which has medial gorget feathers intermediate in color between the violet of *C. anna* and the coppery-red of *S. sasin*. The gorget "tails," however, show a distinct purplish cast, reminiscent of *C. anna*, although not quite as dark as in that species. The color of the remainder of the ventral tracts of hybrids B and C is remarkably like that of *C. anna*, a situation found by Williamson to be true also for Hybrid A. The feathers of the ventral cervical region immediately posterior to the gorget in hybrids B and C are intermediate between the white of *S. sasin* and the brown and gray of *C. anna*. The rufous feather tips typical of the sternal and abdominal regions of *S. sasin* are indicated, in hybrids B and C, only on those barb tips lateral and distal to the median spots of metallic green. Hybrid B seems to show slightly more rufous than Hybrid C in these regions. Hybrids B and C both have considerable rufous on the feathers in the lateral sternal regions, at the bases of the wings, a condition also found by Williamson for Hybrid A.

*Alar tract.*—In *S. sasin* the marginal coverts are buffy with rufous spotting. In *C. anna* these feathers are gray with green spotting. Both hybrids B and C possess green marginal coverts which are edged with rufous or buff. Figure 1 depicts the wings of the two parents and that of Hybrid C. The intermediacy in the shape of the primaries of the hybrid is apparent. Hybrids A and B are like Hybrid C in this respect.

*Caudal tract.*—From the dorsal aspect, rectrices 1-1 of *C. anna* are dark metallic green. Rectrices 2-2 of this species are also metallic, but they are of a darker, more olive-green shade. In addition, these feathers are bordered by dull gray, particularly on the lateral margins. The remaining three pairs of rectrices are nonmetallic, with black along the entire shafts and over most of the feathers near the tips, and with dull gray lateral borders. In *S. sasin* all rectrices are rufous with black of varying extent on their

tips and outer edges (see fig. 3). Only the outermost two rectrices on the left side of Hybrid A remain on the specimen and these have been described and figured by Williamson (1957:119). The distribution of gray, rufous, black, and metallic green on the rectrices of Hybrid B is shown in figure 3. The tails of hybrids A (two rectrices only), B, and C are generally similar both in shade and in extent of color. The tail of *C. anna* is moderately forked, whereas that of *S. sasin* is evenly rounded. The three hybrids display square-tipped tails and are thus intermediate (fig. 3). The shapes of the tips of the

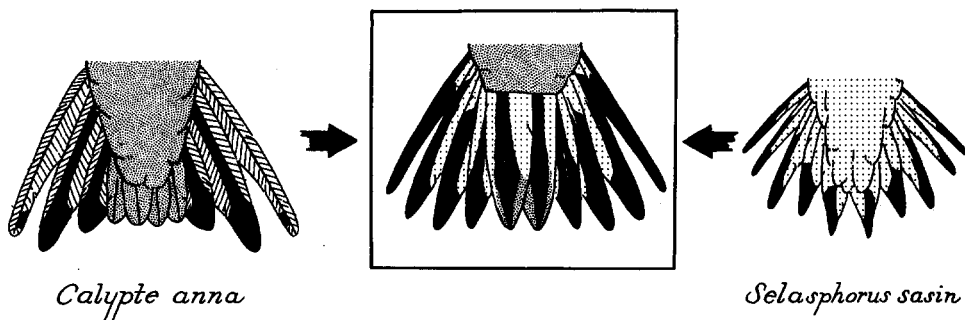


Fig. 3. Color pattern of tails of Anna and Allen hummingbirds and Hybrid B, dorsal view. Solid areas, black; hatching, gray; light stipple, rufous; heavy stipple, green. Upper tail coverts of hybrid are not shown.

rectrices are likewise intermediate between the rounded type of *C. anna* and the pointed type of *S. sasin*. The under tail covert feathers of *C. anna* are green or greenish brown and broadly edged with gray. Those feathers in *S. sasin* are chiefly rufous, showing white basally. The longest median under tail coverts of this species are also tipped with black. Hybrid B has largely rufous under tail coverts with at least two showing broad greenish splotches, as in *C. anna*, and with two median feathers tipped with black. In Hybrid C the under tail covert feathers are similar to those of *C. anna*, but the influence of *S. sasin* is evidenced by rufous edgings. Hybrid A lacks these feathers.

*Notes on Hybrid E.*—Concerning the color and extent of the gorget and crown patch, Macdonald and Goodwin write: "The colour of the gorget is closer to that of *C. anna* . . . showing, principally on the chin and on the sides of the gorget, a little of the golden-red hue of *S. sasin*. This golden-red hue on the type of '*floresii*' is different from and much more pronounced than the very slight tint of gold or copper that *anna* shows in some lights. The iridescent area on the crown does not extend so far back . . . and is, perhaps, slightly less brilliant than in *anna*, although the same colour."

They continue: "The pale fringes of the green feathers of the underparts are paler and more rufescent than those of *anna*. On the flanks and under tail-coverts, the pale edges are more markedly rufous; but the underparts are in general much closer in colour and pattern to *anna* than to *sasin*. The two central tail feathers are dark greenish with some rufous on the inner web; the remaining tail feathers are similar to those of *sasin* in colour and pattern, but with the blackish areas more extensive, especially on the outer webs." The outermost rectrix "is entirely dark except for a tinge of rufous near the base of the inner web." The upper tail coverts are green, not rufous. "The green on the back is intermediate between that of *anna* and of *sasin* and it has a whitish band below the gorget almost (but not quite) as prominent as that of *sasin*."

The tail is stated to be "straight [= square-tipped] or nearly so, so far as one can see

from the skin. It is thus intermediate between the two parent species. The individual tail feathers are also intermediate in shape between those of *anna* and of *sasin*, perhaps a little nearer to those of *sasin*." The outer remex is "intermediate but nearer to that of *anna*, unlike the rectrices; it lacks the sharp point" of the corresponding remex of *sasin*.

This specimen is in "general appearance nearer to *anna* but this effect is largely due to the colour of the gorget, underparts and upper tail coverts . . . as elsewhere it is intermediate." Thus it is evident that Hybrid E is similar in all major features to the other crosses of *C. anna* and *S. sasin*.

*Mensural characters*.—Between *C. anna* and *S. sasin* there are significant differences in length of culmen and in body weight, although the ranges overlap (see table 4). There is no overlap in wing length. In length of the central rectrix (= length of tail in *S. sasin*) the two species are rather similar; the striking differences in tail shape between

TABLE 4

MEASUREMENTS AND WEIGHTS OF ANNA AND ALLEN HUMMINGBIRDS<sup>1</sup> AND HYBRIDS

		Culmen	Wing	Tail	Central Rectrices	Weight
<i>C. anna</i>	Range	16.1-18.4	47.8-51.2	30.1-33.3	23.7-26.1	3.3-5.8 <sup>2</sup>
	Mean	17.4±.14	49.1±.19	31.6±.19	25.0±.15	4.3±.17
Hybrid A		15.6	42.1	.....	.....	3.9
Hybrid B		16.4	42.5	27.8	25.3	.....
Hybrid C		.....	44.6	29.1	27.0	.....
Hybrid E <sup>3</sup>		17.0	45.5	.....	27.5	.....
<i>S. sasin</i>	Mean	15.5±.13	37.9±.13	25.3±.13	same	3.3±.11
	Range	14.1-16.3	36.8-38.8	24.7-26.3	as tail	2.8-3.9 <sup>4</sup>

<sup>1</sup> N = 20 except where noted otherwise.

<sup>2</sup> 16 specimens.

<sup>3</sup> Measurements *vide* J. D. Macdonald.

<sup>4</sup> 11 specimens.

the two forms is a result of the much longer lateral rectrices of *C. anna*. The culmen length of Hybrid A is typical of *S. sasin*, that of Hybrid B is intermediate, and that of Hybrid E is typical of *C. anna*. The bill of Hybrid C is broken. With regard to wing length all four hybrids are intermediate with their values falling between the ranges of the parent species. Weight is available only for Hybrid A, which is nearer *C. anna* in this respect.

## DISCUSSION

### GENETICS OF HYBRIDIZATION

Assuming polygenic action in the expression of individual features of the phenotype, we should observe varying degrees of intermediacy in both the coloration and morphology of F<sub>1</sub> hybrids between two species with contrasting features. Indeed, this is what we have found in the birds examined; in certain characters the hybrids resemble or approach one or the other of the parent species, whereas in other features they are virtually intermediate. Variation in the degree of resemblance to a particular parent is evident in the crosses of *Calypte anna* and *Selasphorus sasin*, the only situation where we have more than one specimen representing a given parental combination.

Certain characteristics of some species seem to be dominant in the crosses, acting in the same way regardless of the other parent. For example, the peculiar squaring of the tips of primaries 5, 6, and 7 of *Stellula calliope* (fig. 1) is evident in both crosses involving the Calliope Hummingbird, as is the character of white-based gorget feathers. The dark chin feathers typical of *Archilochus alexandri* appear on both hybrids involv-

ing that species, dominating the iridescent feathers of the other parents. Throughout the hybrid series, green dominates rufous; this dominance is greater on the body than on the tail. Rufous on the body is largely masked by green in hybrids between *C. anna* and *S. sasin*. The rusty back of *Selasphorus rufus* was dominated by the green of *Stellula calliope* in the hybrid reported by Thayer and Bangs (1907). The rufous tinge on the ventral surface of *Selasphorus platycercus* was masked by the colors of *A. alexandri*. However, some rufous coloration appears on the tails of all crosses involving either *Selasphorus* or *Stellula*.

The iridescent crown of members of the genus *Calypte* usually dominates in hybrids involving a member of this genus, although it is never as extensive on the hybrids as it is on the parental species. This coronal iridescence is evident in *Calypte costae* x *Selasphorus platycercus* (Huey, 1944), *Calypte costae* x *Stellula calliope*, and *Calypte anna* x *Selasphorus sasin*. The hybrid of *Calypte anna* and *Archilochus alexandri*, however, lacks the iridescent crown of *Calypte* and closely resembles the *Archilochus* parent in the color of the head.

#### SEX OF HYBRIDS

As already noted all hybrids considered here are adult males. This is not surprising, because among hummingbird species with strong sexual dimorphism only the males show obvious specific differences in coloration or in shape of the flight feathers. Female individuals produced by the crossing of species whose females are of similar appearance would probably not be readily recognized as hybrids. It is reasonable to assume that interbreeding results in female progeny as often as in male birds, but thus far no female or immature male hybrids have been reported.

#### FREQUENCY OF HYBRIDS

A cursory survey of the literature gives one the impression that hybrid hummingbirds are extremely common. Sibley (1957:176) mentions 37 hybrid combinations in the Trochilidae; Gray (1958) lists 31 combinations. However, of eight combinations listed by Gray involving the North American genera with which we are concerned, two were found by us to be without basis. If the percentage of error is as great in the remaining combinations, the actual number of hybrids is much smaller than the literature would lead one to believe.

There are several factors which help create the impression of an extremely large number of hybrid hummingbirds. One of these is the repetition of listing. Another is the stress placed on hybridization in this and certain other bird groups by persons concerned with evolutionary theory. It must be remembered that hummingbirds have long been of exceptional interest because of their small size and brilliant coloration and so have been the subject of intense study by both professional and amateur ornithologists. There is no question that hybrid hummingbirds are numerous, but fewer exist than is sometimes implied.

Most hybrid combinations are known from only one specimen. An interesting field for speculation concerns the subject of why some hybrid combinations are reported more often than others. Of the seven valid North American crosses discussed here, only one, *Calypte anna* x *Selasphorus sasin*, is represented by more than one specimen. Four of the hybrids of this parentage, and perhaps the fifth as well (Williamson, 1957), were discovered in the San Francisco Bay area.

The fact that only one of these four was collected because it appeared to be something unusual (Emerson, 1901) indicates that the reason for the frequent reporting of this cross is not merely that it is more easily detected. One consideration is that the area

has been, and is, heavily populated by ornithologists. If hybridization is more than an occasional accident, its occurrence in an area would be detected in proportion to the work done there. This may be the case in the San Francisco area.

#### ISOLATING MECHANISMS

Ecologic isolation appears to be an important factor in preventing hybridization between hummingbird species in western North America. Although many species pairs are at least partly sympatric in a geographical sense, it is unusual to find species together locally as breeding birds. Almost always there are ecologic, altitudinal, or seasonal gaps in their breeding distribution. The San Francisco Bay area, where the Anna and Allen hummingbirds overlap ecologically (Pitelka, 1951*b*; Williamson, 1957) is a major exception, and certainly this factor is an important one in the discovery of so many hybrids of this parentage. Williamson also stressed this point (*op. cit.*:118).

Physiological isolating mechanisms, such as interspecific sterility and hybrid inviability or infertility, are important reproductive barriers in many animal groups. The mere presence of a hybrid individual, however, is evidence that the parents were inter-fertile, and the existence of at least eleven hybrid hummingbirds of seven different par-

TABLE 5

DESCRIPTION OF DIVES OF VARIOUS SPECIES OF HUMMINGBIRDS

Species	Shape of dives and flights	Height of dive in feet	Sounds accompanying dive	Source
<i>Archilochus alexandri</i>	"narrow dive," "diving nearly straight down"	20-25	"clear whistling sound in addition to a rattle"	J. M. Linsdale (MS)
<i>Calypte costae</i>	"U-shaped arc some 75-100 feet across"	100-200	"long-drawn-out hissing whistle"	Cogswell (1957)
<i>Calypte anna</i>	"power dives almost vertically downward only to veer sharply upward . . . tracing a long narrow U"	75-100	"sharp, loud <i>peek</i> . . . produced by vibrations of the stiff outer tail feathers"	Cogswell (1957)
<i>Selasphorus platycercus</i>	"vertical dive with wide U"	"40-50"	"3 flups" made by tail at bottom of dive	J. T. Marshall, Jr. (MS)
<i>Selasphorus rufus</i>	as in <i>S. sasin</i>	as in <i>S. sasin</i>	as in <i>S. sasin</i> except lower pitched	A. H. Miller (pers. comm.)
<i>Selasphorus sasin</i>	two phases: "series of shallow swoops along a broad, symmetrical U about 20 to 30 feet across and less than half as high" and "one or two faster, smooth swoops . . . with a veering follow-through"	to 100	"interrupted buzzing" produced by tail  mechanical ripping sound " <i>urrrrp</i> "	Cogswell (1957)
<i>Stellula calliope</i>	"a series of swoops along a moderately shallow, U-shaped course 25 to 30 feet across"	30	"brief, muffled <i>bzzt</i> or <i>pfft</i> "	Cogswell (1957; MS)

ental combinations indicates that interspecific infertility is not an important barrier in the North American representatives of this family. However, we have no idea concerning the effectiveness of this factor in preventing the production of an even larger number of hybrids, if other barriers fail to prevent the formation of interspecific pairs.

The failure of a hybrid to attain reproductive status is, of course, a powerful mechanism in preventing gene flow between parental species even when hybrids are produced. We have little evidence on this point where hybrid hummingbirds are concerned. Of the specimens examined by us, only two have any indication of gonadal condition. The left testis of the hybrid *Archilochus alexandri* x *Selasphorus platycercus* had increased from the winter condition to a size normal for hummingbirds during migration.

TABLE 6

## CLASSIFICATION OF COURTSHIP CHARACTERS OF HUMMINGBIRDS

	Height of dive	Breadth of "U" <sup>1</sup>	Nature of sound	Color of gorget
<i>A. alexandri</i>	Low	Narrow	Prolonged	"Blue"
<i>C. anna</i>	High	Narrow	Short	"Red"
<i>C. costae</i>	High	Broad	Prolonged	"Blue"
<i>S. platycercus</i>	High	Narrow	Short	"Red"
<i>S. rufus</i> <sup>2</sup>	High	Narrow	Prolonged	"Red"
<i>S. sasin</i> <sup>2</sup>	High	Narrow	Prolonged	"Red"
<i>S. calliope</i>	Low	Broad	Short	"Red"

<sup>1</sup> In relation to height of dive.

<sup>2</sup> Second phase of dive.

Williamson (1957) found free sperm in the testicular lumina of the hybrid *Calypste anna* x *Selasphorus sasin* which he studied. Neither of these examples sheds any light on the fertility (functional gametes) of the hybrids, but they suggest that lack of hybrid viability (functional gonads) is not an important isolating mechanism in the Trochilidae.

The combination of distinctive features of gorget color and courtship behavior, including nuptial dives and the sounds produced in conjunction with these dives, would seem to be of potential importance as an isolating mechanism in the Trochilidae. Although Bent (1940:442) states, "The courtship performances of the hummingbirds all follow the same general pattern, with only slight variations," these variations are in fact distinct enough to permit a person familiar with the birds to identify them readily and with certainty. In speaking of hummingbird displays, Sibley (1957:175) states that "by their specificity they can, and probably do, function as species recognition signals and hence as isolating mechanisms."

The paradox of similarity and difference is reflected in table 5, which summarizes many independent descriptions of the courtship displays of the hummingbirds under consideration. All components of these displays are subject to the errors of interpretation by different observers. It appears, however, that the major differences between the nuptial flights of North American hummingbirds are in the height and breadth of the dives and in the nature of the associated sounds. To these differences may be added that of variation in gorget color.

It is possible, using the observations compiled in table 5, to classify these hummingbirds according to characteristics of their courtship flights. Thus in table 6, certain species are considered to be "high divers" whereas others are "low divers"; some species possess essentially "red" gorgets, while in others they are "blue" (or at least "not red"). If these characteristics act as isolating mechanisms, it might be expected that most hybridization would occur between those species which fit into the same categories.

TABLE 7

CLASSIFICATION OF HYBRID CROSSES WITH RESPECT TO COURTSHIP CHARACTERS OF PARENTS

Height of Dive		Breadth of "U"	
High x High	2	Broad x Broad	1
High x Low	5	Broad x Narrow	3
Low x Low	0	Narrow x Narrow	3
Nature of Sound		Color of gorget	
Prolonged x Prolonged	0	"Red" x "Red"	3
Prolonged x Short	6	"Red" x "Blue"	4
Short x Short	1	"Blue" x "Blue"	0

Table 7 shows the crosses in relation to the courting characteristics of the parents. The most striking finding of this compilation is that more hybrids have been produced by parents in different categories than by parents in the same group, except for the character "breadth of 'U'," where the data are inconclusive. The question then arises, to what extent do these factors actually act as isolating mechanisms? Individually, perhaps they do not, but in combination, their effectiveness is probably increased. From table 6 it may be seen that, with the exception of *Selasphorus rufus* and *S. sasin*, no two species are the same in all of their courtship characteristics, and in these species the quality and pitch of the note is different.

TAXONOMIC CONSIDERATIONS

Figure 4 analyzes the hybrid hummingbird combinations considered in this report. It is of interest that all crosses recorded from North America are intergeneric. Furthermore, none of the genera shown in the diagram has been reported interbreeding with

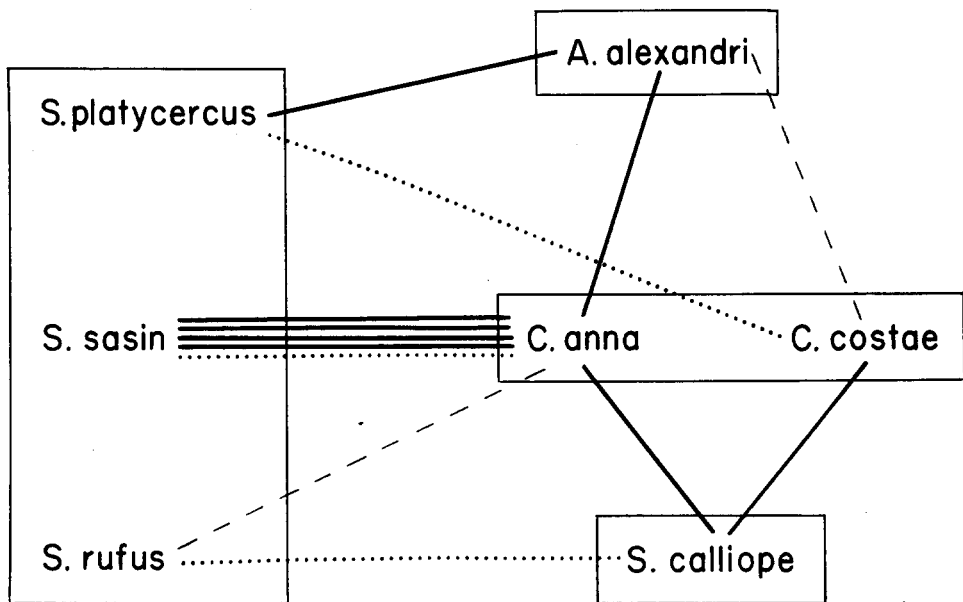


Fig. 4. Diagram of hybridization in North American hummingbirds. Solid lines, extant specimens; dotted lines, specimens lost or destroyed; dashes, crosses reported, but apparently invalid.

genera not included; figure 4 is a closed system. The high proportion of intergeneric crosses in the Trochilidae may indicate, as implied by Taylor (1909), Sibley (1957), and Williamson (1957), that the generic limits in the Trochilidae are artificial and should be revised. On the other hand, it should be considered that the lack of intrageneric hybridization in these North American hummingbirds may result from the perfection of intrageneric isolating mechanisms without the concurrent development of intergeneric isolating mechanisms. Most of the hybrids discussed here are between species which overlap only slightly in geographic range or ecological requirements. The genera *Selasphorus*, *Calypte*, *Archilochus*, and *Stellula* may have arisen from a common ancestral stock at different times. If the meeting of the species of these groups in North America is strictly accidental, as a result of vagrancy, or is of recent origin, as a result of changes in distribution, it may be that there has developed no previous "need" for reproductive isolation between members of different genera. Intrageneric reproductive isolation, on the other hand, would have developed as a natural result of divergence of species from a common ancestor within the genus in the recent past.

These alternative suggestions indicate that a serious study of the generic limits in the Trochilidae is in order. Sibley (*op. cit.*) has emphasized the fact that hummingbird genera are erected mainly on the basis of male characters which have adaptive value in courtship. The problem of the significance of hybridization in hummingbirds cannot logically be discussed until a phylogenetic classification based on conservative characters is established. Although the present generic arrangement of North American Trochilidae may be unsatisfactory, we feel that its retention is practical until such a time as a clearer concept of what actually constitutes a hummingbird genus emerges from future studies of morphology and behavior. Meanwhile, the lack of intrageneric hybrids should be viewed as evidence justifying maintenance of the present generic classification, if the presence of numerous intergeneric hybrids continues to be cited as valid reason for lumping genera.

#### SUMMARY

The North American members of the trochilid genera *Archilochus*, *Calypte*, *Selasphorus*, and *Stellula* have produced at least eleven hybrids of seven different parental combinations. Two additional parental combinations have been listed, but they are apparently invalid. Seven of the eight hybrids known to be extant have been examined by the authors and are described in detail.

Some examples of character dominance have been noted. Rufous is largely masked by green on body feathers, less so on tail feathers. Characters of the interramal region of *Archilochus alexandri* and of the gorget of *Stellula calliope* appear in their hybrids whatever the nature of the other parent involved in the cross. The iridescent red or violet crown typical of the genus *Calypte* is evident in all crosses involving that genus, except in *C. anna* x *A. alexandri*.

Five hybrids between *Calypte anna* and *Selasphorus sasin* have been reported. All other crosses are known only from single specimens.

Ecologic isolation seems to be an important factor in preventing hybridization by North American hummingbirds. Physiological isolating mechanisms are believed to be relatively unimportant. A consideration of gorget colors and courtship displays suggests that no single component is completely effective as an isolating mechanism although the totality of the factors probably is important.

The lack of intrageneric hybridization can be considered as a valid argument for the present generic classification of hummingbirds. Likewise, the presence of intergeneric hybridization can be used as an argument against the present classification. The full



significance of hybridization in North American hummingbirds cannot be determined until the problem of phylogenetic relationships within the Trochilidae is clarified on other grounds.

## LITERATURE CITED

- Aldrich, E. C.  
1956. Pterylography [sic] and molt of the Allen hummingbird. *Condor*, 58:121-133.
- Behle, W. H.  
1943. Birds of Pine Valley Mountain region, southwestern Utah. *Bull. Univ. Utah*, 34:1-85.
- Behle, W. H., Bushman, J. B., and Greenhalgh, C. M.  
1958. Birds of the Kanab area and adjacent high plateaus of southern Utah. *Univ. Utah Biol. Ser.*, 11(7):1-92.
- Bent, A. C.  
1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies. *U. S. Nat. Mus. Bull.* 176.
- Berlioz, J.  
1929. Un cas nouveau d'hybridité chez les Trochilidés. *L'Oiseau et la Revue Francaise d'Ornith.*, 10:340-343.  
1930. A new hummingbird hybrid, *Calypte anna* x *Stellula calliope*. *Condor*, 32:215.
- Bryant, W. E.  
1886. Additions to California avifauna. *Forest and Stream*, 26:426.
- Cogswell, H. L.  
1957. *In* Audubon western bird guide, by R. H. Pough (Doubleday and Co., Inc., Garden City, New York).
- Cockrum, E. L.  
1952. A check-list and bibliography of hybrid birds in North America north of Mexico. *Wilson Bull.*, 64:140-159.
- Emerson, W. O.  
1901. Capture of a Floresi's hummingbird at Haywards, Cal. *Condor*, 3:68.
- Gould, J.  
1861. A monograph of the Trochilidae, or family of humming-birds. Vol. III (Published by the author, London).
- Gray, A. P.  
1958. Bird hybrids (Commonwealth Agricultural Bureaux, England).
- Grinnell, J.  
1908. The biota of the San Bernardino Mountains. *Univ. Calif. Publ. Zool.*, 5:1-170.  
1928. A distributional summation of the ornithology of Lower California. *Univ. Calif. Publ. Zool.*, 32:1-300.
- Grinnell, J., and Miller, A. H.  
1944. The distribution of the birds of California. *Pac. Coast Avif. No.* 27:1-608.
- Hartert, E. J.  
1900. [Exhibition of hybrid hummingbirds.] *Bull. Brit. Ornith. Club*, 10:39-40.
- Huey, L. M.  
1944. A hybrid Costa's x broad-tailed hummingbird. *Auk*, 61:636-637.
- Jeffries, J. A.  
1888. A description of an apparently new species of *Trochilus* from California. *Auk*, 5:168-169.
- Johnson, D. H., Bryant, M.D., and Miller, A. H.  
1948. Vertebrate animals of the Providence Mountains area of California. *Univ. Calif. Publ. Zool.*, 48:221-376.
- Linsdale, J. M.  
1936. The birds of Nevada. *Pac. Coast Avif. No.* 23:1-145.  
1938. Environmental responses of vertebrates in the Great Basin. *Amer. Midl. Nat.*, 19:1-206.

## Miller, A. H.

1951. An analysis of the distribution of the birds of California. Univ. Calif. Publ. Zool., 50:531-644.

1955. A hybrid woodpecker and its significance in speciation in the genus *Dendrocopos*. Evol., 9:317-321.

## Peters, J. L.

1945. Check-list of birds of the world. Vol. V (Cambridge, Mass.).

## Pitelka, F. A.

1951a. Breeding seasons of hummingbirds near Santa Barbara, California. Condor, 53:198-201.

1951b. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecol., 32:641-661.

## Ridgway, R.

1887. A manual of North American birds (J. B. Lippincott Co., Phila.).

1892. The humming birds. U. S. Nat. Mus. Report for 1890:253-383.

1909. Hybridism and generic characters in the Trochilidae. Auk, 26:440-442.

1911. The birds of North and Middle America. Bull. U. S. Nat. Mus. 50, pt. 5.

## Rothschild, L.

1927. [Exhibition of hybrid hummingbirds.] Bull. Brit. Ornith. Club, 48:41.

## Sibley, C. G.

1957. The evolutionary and taxonomic significance of sexual dimorphism in birds. Condor, 59:166-191.

## Sibley, C. G., and Short, L. L., Jr.

1959. Hybridization in some Indian bulbuls *Pycnonotus cafer* x *P. leucogenys*. Ibis, 101:177-182.

## Simon, E.

1910. Notes critiques sur les Trochilides. Rev. Fr. Ornith., 2:177-178.

## Taylor, W. P.

1909. An instance of hybridization in hummingbirds, with remarks on the weight of generic characters in the Trochilidae. Auk, 26:291-293.

## Thayer, J. E., and Bangs, O.

1907. Another hybrid hummingbird—*Selasphorus rufus* + *Atthis calliope*—from California. Auk, 24:312-313.

## Williamson, F. S. L.

1957. Hybrids of the Anna and Allen hummingbirds. Condor, 59:118-123.

*Museum of Vertebrate Zoology, Berkeley, California, June 2, 1960.*