HYBRIDIZATION IN CALYPTÉ HUMMINGBIRDS

SHIRLEY WELLS,1 RICHARD A. BRADLEY,2 AND LUIS F. BAPTISTA3

ABSTRACT.—We describe 11 individuals probably representing a new hybrid combination between Anna’s Hummingbird (Calypte anna) and Costa’s Hummingbird (Calypte costae). The probable hybrids are intermediate in morphology but more closely resemble Costa’s Hummingbird. The behavior of the suspected hybrids is intermediate but the song is typical of Anna’s Hummingbird. These probable hybrids represent the first known intrageneric hybrid combination among North American hummingbirds. Although taxonomic revision of North American hummingbirds is in order, more work is needed before such changes are made. Received 10 May 1977, accepted 18 July 1977.

HYBRIDIZATION among North American hummingbirds has been reviewed by several authors (Banks and Johnson 1961, Short and Phillips 1966, Lynch and Ames 1970, Mayr and Short 1970). These authors have noted the lack of intrageneric hybrids in the context of current classification.

During the past few years studies of suburban populations of hummingbirds in southern California have revealed a new hybrid combination. Eleven individuals have been located that seem to represent hybrids between Calypte anna (Anna’s Hummingbird) and Calypte costae (Costa’s Hummingbird). The discovery of these hybrids in suburban-residential areas may not be coincidental. It is just such disturbed heterogeneous habitats that allow for syntopy in species that are not normally found in the same localities. Anna’s Hummingbird is a common resident in many southern California habitats, nesting in coastal sage, chaparral, oak woodland, and riparian edge; for more information on this species’ ecological relationships in southern California, see Stiles (1973). Costa’s Hummingbird is mainly a summer visitor in southern California and nests in drier coastal sage habitats inland, as well as desert scrub edge and Sonoran desert. Costa’s Hummingbirds are also present in small numbers in these habitats each fall and winter. Some males begin to display as early as October. In natural environments the two species rarely occur together. The ranges of the two species are illustrated in Fig. 1.

In the following account all birds believed to be hybrids, based on external morphology or behavior, are usually referred to as hybrids for brevity. All of the presumed hybrids were males. We have no evidence of any backcross hybrids.

HISTORY OF THE HYBRIDS

The first substantiated hybrid was an individual captured and banded (X-12663) on 11 September 1970 on the Palos Verdes Peninsula, Los Angeles County, California. This bird was not captured again. Diagnostic feathers and measurements were obtained. A second individual was captured at Palos Verdes, banded (X-13305), and released on 24 July 1971. This bird was recaptured on 28 August 1971, died, and was prepared as a study skin at the Los Angeles County Museum (LACM 78608). A third individual was captured at Palos Verdes, banded (X-13311), measured, and released on 25 July 1971 in immature plumage. This bird was re-

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537 The Auk 95: 537–549. July 1978
Fig. 1. The distribution of Calypte hummingbirds. The horizontal ruled portion is the approximate breeding range of C. anna. The vertical ruled area is the approximate breeding range of C. costae. The numbered dots indicate localities where presumed hybrids were located: 1, Paradise; 2, Pierce College; 3, Monterey Park; 4, South Coast Botanic Gardens (2 individuals); 5, Palos Verdes Peninsula (4 individuals); 6, Huntington Beach; and 7, Sunnymead.

captured in adult plumage on 22 October 1971, 29 July 1972, and 2 September 1972. An immature male was collected on the Palos Verdes Peninsula on 21 July 1972 (LACM 18874). It was recognizable as a hybrid from the appearance of emerging gorget feathers and intermediate measurements. One additional specimen was located in the collections of the Western Foundation for Vertebrate Zoology (WFVZ 19750); this bird was collected during 1975 at Pierce College, Los Angeles County, California. To date, six additional probable hybrids have been observed in the field. Two were discovered at the South Coast Botanic Gardens, Palos Verdes Peninsula, Los Angeles County, California. These individuals were the subjects of our observations of displays and recorded vocalizations. One individual (#1) was first seen in the winter of 1971. What was probably the same bird held the same territory up to 1976 when observations ceased. A second bird (#2) was first seen in January
Fig. 2. Views of *Calypte* males in the static display pose: A, *Calypte anna*; B, hybrid; C, *Calypte costae*.

1974. It held a territory through April of 1974. Hybrid #1 was sometimes on territory as early as September and remained until late March or April. Display was not noted from the hybrids after March. Most *Calypte anna* territories break down by late February and the individuals cannot be relocated until the following fall.

E. N. Anderson, Jr. (pers. comm.) discovered a possible hybrid on 2 February 1972 at Sunnymead, Riverside County, California. He described a hummingbird that came to his feeder as intermediate in body size, color, and shape of gorget between Anna's and Costa's hummingbirds. He described its “chip” (we use “tick”) note as dry and thin like Costa’s, but a bit toward Anna’s and considered the song identical to that of Anna’s. Its singing perch was about 4 m high; the tendency to perch relatively high, Anderson suggested, is a characteristic of Anna’s rather than of Costa’s. One of us (Wells) visited Sunnymead on 21 February 1972, 20 March 1972, and 14 February 1974, saw the hybrid, confirmed Anderson’s diagnosis, and

### Table 1. Measurements of *Calypte anna* and *Calypte costae* adult male specimens that were collected in southern California. All length measurements in millimeters

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*a* Length of iridescent portion of longest feather in gorget tail
heard the bird singing its Anna-like song. This individual was closer to Costa's in appearance.

Wells and Grace Nixon observed a hybrid perched on a low shrub in an oil field near a golf course in Huntington Beach, Orange County, California on 17 December 1972, and again on 3 and 14 January 1973. As with our specimens, this individual was similar to Costa's Hummingbird in appearance but sang an Anna-like song.

On 24 August 1973, Bruce Webb described what he suspected to be a hybrid Anna's × Costa's at his feeder at Paradise, Butte County, California. He had captured the bird on 5 August, taken measurements, removed its rectrices and released the bird. Measurements are as follows: culmen 17.5 mm, wing chord 47.5 mm, tail 23.0 mm. The culmen is within the range for Costa's, but closer to the mean for Anna's (Table 1). The tail (rectrix 1) and wing chord are intermediate between those
of the two presumed parental species. Webb kindly sent the rectrices to Wells, who confirmed his opinion that it was indeed an Anna's x Costa's hybrid. Paradise is 320 km north of the known range of Costa's Hummingbird.

Wells carefully observed another individual on 9 and 10 January 1974 at Monterey Park, Los Angeles County, California. The song was Anna-like and the bird was intermediate in appearance. Both parental species were present for comparison. This bird remained for less than a week and was not observed thereafter. All of the localities mentioned above are shown in Fig. 1.

MORPHOLOGY

The hybrid males were compared with adult males of both presumed parental species. The description given here represents a composite from the two individuals banded and released, as well as the specimens in the Los Angeles County Museum and the Western Foundation for Vertebrate Zoology. In addition, the feathers plucked from the two banded birds and photographs were used in the description.

Capital tract.—Except for the occipital and auricular regions, the entire head of Calypte anna is "metallic rose red, changing to solferino and violet in certain lights" (Ridgway 1911:619). The corresponding parts in costae are generally more violet-blue. The color of the hybrid’s crowns are intermediate, definitely tending more towards costae.

The gorget shape and color differ in the two parental forms; the lateral extensions of the throat (the “tails” of Banks and Johnson 1961) are longest in costae, shortest in anna, and of intermediate length in the hybrids (Tables 1 and 2, Fig. 2). The central portion of the gorget beneath the chin extends further down the throat in anna than in costae and is intermediate in the hybrids, but resembles costae (Fig. 2). Each gorget feather of the lateral tails is divided into an iridescent distal portion and a duller basal portion. The junction between metallic and dull portions in costae is “V” shaped, rounded in anna, and intermediate in the hybrids (Fig. 3). There is a narrow band of green separating the metallic violet portion from the dull gray basal portion. This green band is wider in costae than in anna and of intermediate width in the hybrids.

The white postocular stripe is broadest and brightest in costae, narrowest and dullest in anna, and intermediate in the hybrids. This stripe is slightly brighter in the WFVZ specimen.

Spinal tract.—This is metallic bronze green from the occiput to the tip of the tail in both parental species. It is our impression that in fresh specimens the green is slightly bluer in anna. The hybrids tend toward anna in this character.
**Ventral tract.**—The lower throat (immediately posterior to the iridescent gorget) and upper breast is grayish-white in *costae*, dusky in *anna*, and intermediate in the hybrids, but tending more toward the white of *costae*. The sides and belly in both parental species are metallic green, which is darker and more dusky in *anna*. The WFVZ hybrid is pale green on the sides like *costae*, but dark green on the belly like *anna*. The adult LACM hybrid is similar below to the WFVZ specimen, but the center of its belly is lighter, tending towards *costae*. The grayish-white breast patch described for *costae* continues as a narrow streak down the center of the belly. This streak is absent in *anna* but present in the hybrids. The longest (central) pair of undertail coverts are more gray with darker gray centers in *anna* and lighter gray or white in *costae*. The WFVZ hybrid is closer to *costae* in this character, while the adult LACM hybrid is closer to *anna*.

**Caudal tract.**—The outermost rectrix (number 5) is narrow in *costae*, wider in *anna* and of intermediate width in the hybrids (Tables 1 and 2, Fig. 3). Rectrix number 1 (central) is similar in shape in all three forms, but widest and longest in *anna*, narrowest and shortest in *costae* and intermediate in the hybrids (Fig. 3).

Rectrix number 2 is uniformly green in *costae* but edged with gray on inner and outer webs in *anna*, beginning one-third of the way below the distal tip and continuing on to the base of the feather (Fig. 3). In a few specimens this lighter edging is light rufous as reported earlier by Williamson (1957). On the hybrids this character is intermediate but more similar to *anna* (the gray edging is just visible) than to *costae*.

In *Calypte* rectrix number 5 is much narrower than the other tail feathers. This may have some functional significance in sound production. In *anna* rectrix 5 is relatively straight with an obtuse end. In *costae* rectrix 5 is slightly curved medially and is almost entirely gray on its inner web. Rectrix 5 in the hybrids is intermediate (Fig. 3).

**Behavior**

There are two kinds of hummingbird displays: (1) vocal and visual displays associated with perched individuals sometimes called the “static” display, and (2) all of the aerial or “dynamic” displays and associated sounds.

The static displays in *Calypte* include at least two types of vocalizations as well as a visual display. In the visual display a male sits on an exposed perch and spreads his gorget, which is then “displayed” to territorial rivals (or females?) by slowly turning the head (this causes the iridescence to flash). The visual display is frequently accompanied by the “song” of these hummingbirds. In *Calypte anna* the song is very complex and relatively loud. This song ranks among the most complex of all hummingbird songs and may well be as acoustically complicated as any in nonpasserine birds. The song may last over 3 s and contain 18 or more complex utterances of several types (Fig. 4). In addition to the song, *Calypte* males also give a short “chip” or “tick” note while engaging in the visual display. Static displays apparently function primarily for territorial advertisement to other male hummingbirds. Not only conspecifics but a variety of other species may be the target of such displays. Anna’s Hummingbirds in southern California attack hummingbirds of several other species that intrude into their territories, including *Archilochus alexandrii* (Black-chinned), *Calypte costae*, and *Selasphorus sasin* (Allen’s). Females do not seem to be attracted to the static song display, at least in *C. anna*. Woods (1927) stated that male *C. costae* may sing to “salute” conspecific females. In such cases the males hover in
front of their potential mates. The true static display song is purely territorial in its function (Pitelka 1951, Williamson 1956).

Aerial dynamic displays in Calypte are of two types. The first is the courtship dive. This display is typically performed by the male and may also be used as a territorial display where it is directed toward either sex in conspecifics or even other species (Pitelka 1942, 1951; Williamson 1956). For example, male C. anna have been observed displaying to female S. sasin as well as females of C. costae. The dynamic display sounds will be discussed separately for each species. It is clear that some vocal component is involved in certain displays.

Another display associated with agonistic encounters is the aerial chase. In Calypte this is a rapid zigzag flight with a chattering vocalization. Males and females may play either role in this display. During certain seasons the females are more frequently the aggressors. At hummingbird feeders during the non-breeding season females frequently chase males away from these preferred feeding sites. The object of an aerial chase may or may not be a conspecific.

Calypte anna

The territorial song in Calypte anna is relatively loud and complex (Fig. 4). Males of this species deliver this vocalization regularly throughout the year. Annual peaks of song activity usually occur during the period preceding courtship. This may be as early as mid-October in some years at Palos Verdes (Bradley and Wells, pers. obs.). The songs of various males of this species show little variation in their pattern. The length of any particular individual's song does vary somewhat. Birds from an insular population studied by Mirsky (1976) used songs with a very different structure.
In addition to the song, _C. anna_ also utter a loud “chip” or “tick” call from a song post while giving the visual display. This sharp note is illustrated in Fig. 5A. The specific function of the note is unclear to us, but it may serve as a low intensity advertising display or location note (Stiles 1971). The same note is sometimes used by either sex while foraging and is especially evident around artificial feeders.

The courtship dive or dynamic display in _C. anna_ is dramatic and has been described in detail by Hamilton (1965). A male will rise up to a height of 25–50 m over a female perched in vegetation. As the male ascends he continues to look down (bill pointed straight down). The male pauses at the top of his climb for an instant then dives at an angle, swooping out of his dive just over the female. Just as he reaches the bottom of this power dive a sharp chirp sound is produced. The male then ascends for another display dive. Usually he pauses a few feet up, hovers over the female, and sings the typical song of this species. The male ascends as before (bill pointed down) to approximately the same position and repeats the performance (Fig. 6A). It is not known whether the chirp sound is produced vocally, mechani-
Fig. 6. Illustrations of the dynamic display in *Calypte* hummingbirds: A, *C. anna* dive; B, *C. costae* dive; C, hybrid "costae-like" dive; D, hybrid "typical" dive. The drawings of the hybrid dives were based upon observations of bird #2.
Fig. 7. Sonogram of a hybrid male’s song made from recordings of bird #2.

cally, or has components of both. Several authors have assumed that the sound was produced by air rushing through the tail feathers at this highest speed portion of the dive (Miller 1940, Rodgers 1940, Wagner 1966). Most of the peculiar mechanical display sounds documented for hummingbirds are produced by the wings. *Calypte* males do not produce any discernible wing whir or ringing sounds during normal flight, in striking contrast to the males of *Selasphorus*. We have not observed males of *C. anna* “sing” their dive chirp sound while sitting in the static display posture.

**Calypte costae**

The territorial song in *C. costae* is relatively simple when compared to that of *C. anna*. It can be described as a high-pitched whistling sound. Woods (1927) described the song as a “two or three syllabled whistling call” (Fig. 5E). Males of this species also use a single whistle song (Fig. 5D) similar to the sound produced at the climax of the courtship display (Fig. 5F). Young males of *C. costae* apparently sing more frequently, as well as use a more complex song. The song of these first-year birds approaches the complexity of male *C. anna* songs (Stiles, pers. comm.). Woods (1927) also stated that young (first-year) male Costa’s may sing a song that resembles the song of adult Anna’s, but is “fainter and less sustained.”

Costa’s Hummingbirds also produce “tick” notes similar to those described for *C. anna*, but high pitched (Stiles 1971). In the Anna’s Hummingbird, females also use this call, the specific function of which is not known. Costa’s Hummingbirds produce a rapid chatter, similar to that of Anna’s, during agonistic aerial chases. This aggressive song is more musical (tonal) and less harsh than that of *C. anna* (Wells, pers. obs.).
The dynamic display dive in *costae* is much like that in *C. anna*, but consistent
differences are evident. The most obvious difference is the sound that is produced.
In *costae* the sound is a shrill whistle that lasts approximately 2 s (Fig. 5F) and is
produced through most of the oval-shaped dive path, unlike the short report char-
acteristic of *C. anna*. The sound is presumably vocal since a nearly identical whistle
sound is made by male *C. costae* perched in the static display (Fig. 5D) (contra
Wagner 1966).

The display dive itself also differs from that of *C. anna*. The males of *C. costae*
do not pause or sing after the dive but ascend directly and dive again. During intense
display bouts there is no discernible pause, and the effect is of the male Costa’s
flying an oval-shaped path (Fig. 6B). The dive arc of *C. costae* is much wider than
that of *C. anna*. Males of *C. costae* ascend for the display dive with their bill pointed
slightly upward (Fig. 6B).

**HYBRIDS**

The static display song of hybrid male #1 was similar to that of *C. anna* males.
It was long and complex with an even scratchier quality. The harsh quality is due
partly to the weaker nature of the song and partly to the slightly higher pitch (Fig.
7). The songs of hybrids are well within the normal range of Anna’s and unlike
those of divergent insular populations (Mirskey 1976). The behavior of the hybrid on
his singing perch was much like that of *C. anna*. He aggressively chased all intruders,
including *C. anna*, *C. costae*, and *Selasphorus sasin* males. During such agonistic
encounters he used a rapid chattering vocalization similar to that of *C. anna*. The
“tick” note of hybrid males sounds intermediate in pitch, between that of *C. anna*
and *C. costae*.

The courtship display dive exhibited by the hybrids that we observed is unique.
The display begins as in *C. anna*. The male ascends, bill pointed down, slowly to
the top (approximately 40 m high) then swoops down in a wide arc almost like a
male *C. costae*. During the bottom one-third of the arc a squeak sound is produced.
This sound is not as short or sharp as the chirp of *C. anna* yet not as extended,
high-pitched, or thin as that of *C. costae* (Fig. 5). On audiospectrograms the “chirp”
of *C. anna* appears to have a rich harmonic structure (Fig. 5B), while the dive
sounds of *C. costae* and the hybrid are tonally pure. The bird then ascends again
and pauses at the top of the display. At this point he flies a flat clockwise circle
approximately 16 m in diameter. When the male has scribed the circle and returned
to the original position he dives again (Fig. 6D). The presence of a circle at the top
of the display flight is very unusual. It has been observed in each of the five hybrids
studied in the field. While Baptista was recording what he presumed to be “pure”
*C. costae* at Anza Borrego State Park, San Diego County, California, he saw an
individual flying in a small circle at the top of his display during 19 consecutive
displays. This bird was not collected, but his vocalizations appear to be typical of
*C. costae* (Fig. 5). To our knowledge the circle flight does not occur normally in
either *C. anna* or *C. costae* courtship displays. The size of the circle at the top of the
courtship display varies. In one hybrid male the circle was quite small, approxi-
mately 4 m in diameter. In another male the circles were about 17 m in diameter.
At least two of the hybrid males sometimes omitted the circle at the top of the
display (Fig. 6C). On these occasions the display flight closely resembles the simple
oval path typical of *C. costae* males (Fig. 6B). The height at the top of the display
flight is also variable. In most cases it was approximately 40 m. The height of the perched female may explain some of the variation, although some male Costa’s ascend to 50 m or more over females perched in low vegetation.

**DISCUSSION**

We have described herein what appears to be a new hybrid combination of hummingbirds. Although intermediate in many morphological characters, all birds are closer to *costae* in appearance. All five birds heard sang *anna*-like songs.

Hybridization between two species would presuppose some overlap in the breeding seasons of the parental forms. On the Palos Verdes Peninsula, nests of *costae* with fresh eggs or nestlings have been recorded from November 30 to June 23, and for *anna* from December 22 to May 26 (Wells, pers. obs.).

Hybrids also tend to occur when individuals of one parental form are relatively rare so that conspecific mates are in short supply. An intense banding program conducted by Wells between 1970 and 1973 supported field observations that the numbers of *costae* declined from 1970. In 1970 30 *costae* were banded, while in 1973 none were captured. The numbers of *anna* banded varied from 57 in 1970 to a high of 101 in 1972 and then 42 in 1973. Some of the decline is attributable to a decline in banding effort, but the major drop in *costae* is related to habitat disturbance. This alone would not account for the apparently regular hybridization, since hybrids occurred even in 1970 prior to the decline. However, the data support observations of field observers that *costae* were never as abundant as *anna* at these localities, thus setting the stage for mixed pairing.

**Displays.**—Behavior patterns may appear or disappear through time, as do morphological characters. It is believed that behavior patterns do not disappear altogether, but that due to selective pressures new genes may raise behavioral thresholds so that certain action patterns may be rarely expressed (Manning 1964, Kaltenhäuser 1971). Dispositions to perform those action patterns are therefore still preserved in the genome in a latent fashion. In studies of avian hybrids, behavior rare or absent in the parental forms, and/or typical of closely related species, may be quite common in hybrids (Lorenz 1958, Buckley 1969, Kaltenhäuser 1971). The new genotype in the hybrids presumably results in lowering of behavioral thresholds permitting frequent expression of the “atavistic” action patterns. The horizontal circle flight typical of *anna × costae* hybrids, extremely rare in *costae* and absent in *anna*, may be an example of this phenomenon. We are also mindful that the *costae* with the aberrant display may have been a hybrid.

**Generic limits of hummingbirds.**—The description of these intrageneric hybrids brings the total number of known hybrid combinations of North American hummingbirds to at least twelve. Intergeneric hybrids have been taken as evidence of close relationships between hummingbird genera, and authors have suggested that perhaps too many genera are currently recognized. Mayr and Short (1970) have proposed merging *Calypte* into *Archilochus*. Short and Phillips (1966, see also discussion in Selander 1971) argued that because of a superfluous number of hummingbird genera, congeneric species are usually allopatric so that intrageneric hybrids are less probable. Banks and Johnson (1961), working with trochilid hybrids, and Parkes (1961), working with piprid (Pipridae) hybrids, independently concluded that intergeneric hybrids are more likely to occur in nature than are intrageneric. They proposed that barriers to hybridization may be less stringent once generic status is
reached. Although we agree with all the above authors that a review of the hummingbird genera is in order, we share the view of Banks and Johnson (1961) that until we know more about the morphology and behavior of hummingbirds and can define conservative phylogenetic characters, the genera of North American hummingbirds should not be tampered with.

ACKNOWLEDGMENTS

We thank Ned K. Johnson (Museum of Vertebrate Zoology, University of California, Berkeley), Ralph Schreiber, and James Northern (Los Angeles County Museum) for loan of specimens under their care; Lloyd Kiff for calling our attention to, and the generous loan of, a hybrid in the Western Foundation of Vertebrate Zoology; Grace Nixon who helped in so many ways and for cheerful companionship in the field. We also thank Nancy Halliday for preparing illustrations for Figs. 2 and 3 and Glen Rogers for Fig. 6A–D.

LITERATURE CITED