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DISPLAYS AND MORPHOLOGY OF AN ANNA × ALLEN HUMMINGBIRD HYBRID

SHIRLEY WELLS[1] AND LUIS F. BAPTISTA

Hybrids between the Anna (*Calypte anna*) and Allen (*Selasphorus sasin*) hummingbirds have been reported by a number of authors (Williamson 1957, Banks and Johnson 1961). Displays and vocalizations of such hybrids have hitherto not been described. Moreover, all hybrids discovered so far have presumably involved the migratory *S. s. sasin* as one of the parents. We report here the first record of a hybrid between *C. anna* and the non-migratory *S. s. sedentarius*, describe its displays and vocalizations, and discuss the ecological circumstances which may have permitted hybridization between the 2 parental forms.

HISTORY OF THE HYBRID

The hybrid was first observed on 9 March 1976, in the South Coast Botanic Garden, Palos Verdes Peninsula, Los Angeles Co., California (map in Wells, Bradley and Baptista 1978). It was observed chasing a number of Allen Hummingbird males that held adjacent territories.

The hybrid was netted on the evening of 15 March and ringed with a U.S. Fish and Wildlife Service aluminum band. At that time, kodachromes of all diagnostic features, notes, measurements and weight were taken. A few feathers showing diagnostic features were removed for preservation from the gorget, including longest right and left "gorget tails," from among the longest undertail coverts, and from the upper tail coverts, breast and vent. These have been deposited in the Moore Laboratory of Zoology (ML66272). We did not remove the outermost rectrix, a most important diagnostic feature, so as not to impede in any way the displays of the hybrid. However, shape and color of the rectrices are shown very clearly on our color prints (H2 in Fig. 1).

The hybrid was released at 10:55 on 16 March. Its territory meanwhile had been taken over by an Allen Hummingbird. The hybrid subsequently moved to another part of the garden where it was located on 2 April and was studied periodically until 21 April.

DESCRIPTION OF HYBRID

This description is based on detailed notes, made when the hybrid was in hand, aided by kodachromes showing all the diagnostic features. Color of gorget also is based on a few feathers from the hybrid and compared with museum specimens of the parental forms. Specimens of the latter were taken from March to December and, therefore, included at least some specimens in comparable state of feather wear with the hybrid.

Capital tract.—Gorget color of *C. anna* is metallic rose red, changing to solferino and violet in certain lights (Ridgway 1911:619). Gorget color

[1] Deceased.

in *S. sasin* is more orange (coppery) red. Gorget color in the hybrid was intermediate, tending toward *anna*. Feathers at the base of the hybrid's bill were rufous, a few with green centers. This last feature was also found in Williamson's (1957) hybrid.

Iridescent gorget feathers are confined to the throat in *S. sasin*, but extend over the forehead and crown in *C. anna*. Gorget shape in the hybrid was similar to *C. anna*. However, the iridescent purple feathers in the hybrid did not extend as far back over the head as in *anna*. In the hybrid, feathers in the loral, superciliary and auricular regions were tinged with rufous, characteristics of *sasin*. This was similar to hybrid B of Banks and Johnson (1961). The white postocular stripe of both parental forms was also present in the hybrid.

Spinal tract.—The nape, back and rump are metallic green in *anna*. In *sasin*, the nape and back are rufous-tipped and the rump is entirely rufous. The hybrid was green throughout, except for slight hints of rufous tipping the rump feathers.

Ventral tract.—Gorget "tails" are 12–13 mm in both parental forms. The right gorget tail measured 12.8 mm in the hybrid. The iridescent portion on the gorget tail in *anna* measures approximately 5 mm (N = 22). The latter is 4 mm in *sasin* (N = 13) and 5 mm in the hybrid. The basal portion of the iridescent gorget feathers in *anna* is uniformly gray. These feathers have a broad (2.5–3 mm) band of rufous bordering green-gray in *sasin*. In the hybrid the rufous band was narrower than in *sasin* and was gray basally.

Feathers immediately below the gorget in the hybrid were whitish, reminiscent of *sasin*. In *anna* these feathers are grayer. In the hybrid, feathers of the sides and flanks were metallic green with tinges of rufous, the latter a character of *sasin*.

Alar tract.—The leading edge of the wing was rufous in the hybrid. Underwing coverts were green, some feathers edged with rufous. There was a large rufous patch in the axilars. The rufous areas are all *sasin* characters.

Caudal tract.—Dorsally, rectrix 1 is metallic green in *anna*. Rectrix 2 is less metallic and edged with gray in inner and outer webs. The latter may be buffy in a few specimens as noted earlier by Williamson (1957). All other rectrices in *anna* are black with grayish edges. All rectrices in *sasin* are rufous with various amounts of black on the distal tips and outer edges. Rectrices of the hybrid were similar in color and shape to those illustrated in Banks and Johnson (1961) and were intermediate in shape between the parental species. Rectrix 1 in our hybrid differed slightly in coloration from Banks and Johnson's (1961) specimen in that the green extended farther down the shaft in our bird (compare H1 and H2, Fig. 1).

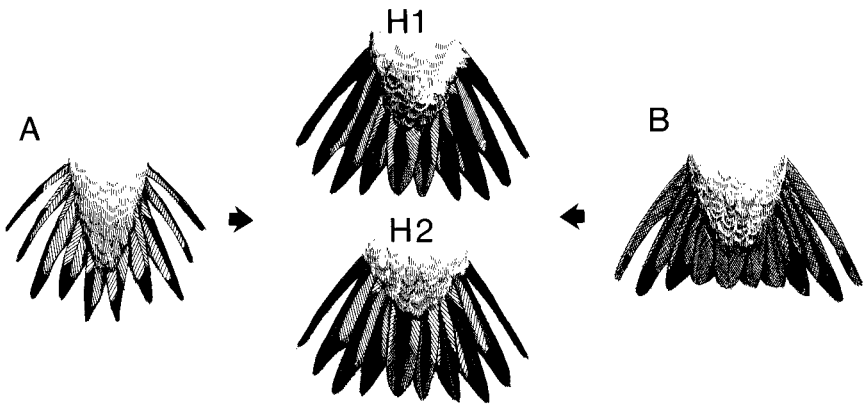

FIG. 1. Tails of (A) *Selasphorus sasin*. (B) *Calypte anna*. (H1) Hybrid *Calypte anna* × *Selasphorus sasin* from Banks and Johnson (1961). (H2) Hybrid *Calypte anna* × *Selasphorus sasin sedentarius* from this study drawn from kodachromes. Note more green (cross-hatching) on rectrix 1, and more rufous on rectrix 4 (diagonal lines) in our hybrid compared to Banks and Johnson (1961).

Undertail coverts in *sasin* are rufous but green or greenish-brown in *anna*. Undertail coverts in the hybrid were green edged with rufous. The longest pair of undertail coverts was black-tipped in Banks and Johnson's (1961) specimen, light green-tipped in our hybrid.

Measurements of the hybrid.—There is overlap between *S. sasin* and *C. anna* in all measurements. However, if only means are considered, the hybrid is intermediate in wing length and weight between *S. s. sedentarius* and *C. anna* (Table 1). Bill length of our hybrid is longer than means for either alleged parental type. It falls within the range of *sedentarius* and *anna*, but beyond that for nominate *sasin*.

EPIGAMIC DISPLAYS

Dive Displays

C. anna.—The dive display of the Anna Hummingbird has been described by a number of authors (review in Wells, Bradley and Baptista 1978). Briefly, the male flies upward 75–150 ft (22.8–45.5 m) above the female with his bill pointed down, sometimes pausing there to sing, then he flies still higher. At the top of his climb he pauses a second time, looking down at the female, often singing once more. He then dives over the female making a sharp *peek* (terminology after Cogswell 1957) (Figs. 2A and 4C) at the bottom of the dive. Thereafter, he may repeat the display, fly after the female, or fly to a perch and sing.

S. sasin.—The following description is from Bassett (1921) and Banks

TABLE 1
MEASUREMENTS OF HYBRID ANNA × ALLEN HUMMINGBIRD AND MALES OF THE PARENTAL TYPES

	N	Culmen	Wing	Weight
Selasphorus s. sasin[1]	20	14.1–16.3 (15.5 ± 0.13)	36.8–38.8 (37.9 ± 0.13)	2.8–3.9 (3.3 ± 0.11)[2]
Selasphorus s. sedentarius[3]	13	17.0–18.8 (17.62 ± 0.58)[b]	38.0–39.5 (38.73 ± 0.49)[b]	3.2–3.81 (3.52 ± 0.24)[a]
Calypte anna[1]	20	16.1–18.4 (17.4 ± 0.14)	47.8–51.2 (49.1 ± 0.19)	3.3–5.8 (4.3 ± 0.17)[4]
Hybrid 5[3]	1	18.6[5]	43.5	3.85

Values in brackets are means ± 1 standard deviation.
[a] One-tailed *t*-test, $P < 0.005$ when compared with nominate subspecies.
[b] One-tailed *t*-test, $P < 0.0005$ when compared with nominate subspecies. (One-tailed *t*-tests were used to demonstrate that Palos Verdes birds were larger than the nominate.)
[1] Data from Banks and Johnson (1961).
[2] 11 specimens.
[3] Data from this study, material from Palos Verdes, California, the *sedentarius* data are from live specimens subsequently banded and released.
[4] 10 specimens.
[5] Note that this value is much larger than the range for the nominate form, indicating *sedentarius* as one of the parental forms.

and Johnson (1961) supplemented with our notes. The male *sasin* flies back and forth over the female, tracing arcs 20 to 30 ft (6.1–9.1 m) across. At the end of each arc (points b and c in Fig. 2B) the male spreads his tail and shakes violently, making a high pitched (7.5 to 12 kHz) chirruping sound (Fig. 3A), lasting about 0.8 sec. After a number of these horizontal arcs, he flies upward 75 to 100 ft (22.8–45.5 m). During the climb his bill is pointed upward and his flight is slow and heavy, "describing spirals or undulations until he reaches the top" (Bassett 1921:37). Without pausing at the zenith, he then dives. Pearson (1960) has computed the speed of flight at various parts of the dive as varying from 34 to 64 mph (54.4–102.4 kmph). At the bottom of his dive he makes a mechanical ripping sound, *tup tup tup trrrr*! On the audiospectrograph this appears as an interrupted whistle at about 1.75 kHz with overtones at 3.5 and 5.25 kHz (Fig. 4A). The entire display may be repeated a number of times, or he may fly after the female. This display also is used against intruders. The displayer sometimes changes the direction of his horizontal arcs in the middle of his display (Baptista, pers. obs.).

C. anna × *S. sasin*.—The hybrid flew upward some 50 ft (15 m). During ascent his bill was pointed down as in *anna* but he traced an undulatory path similar to *sasin*. The bird sometimes paused at the zenith with bill pointing downward for 3–8 sec as in *anna*, or dived immediately as in

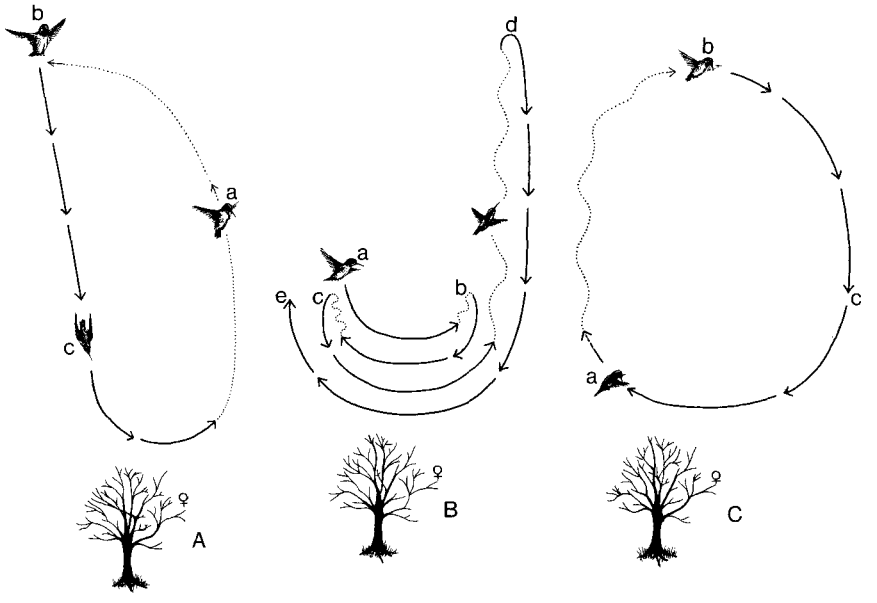

FIG. 2. (A) Display of *Calypte anna*, modified from Wells, Bradley and Baptista (1978). (B) Display of *Selasphorus sasin*, modified from Bassett (1921). (C) Display of Anna × Allen hybrid.

sasin. The arc at the top of the climb is much rounder in the hybrid than in either parental type (Fig. 2C). At the bottom of the dive it made a "pop" sound.

The "pop" sound is very similar to *sasin* in morphology and spectral structure, with a fundamental interrupted whistle at 1.75 kHz and overtones at 2.75 and 4.75 kHz (Fig. 4B). Its temporal structure, however, is very similar to *anna*. At no time was it heard singing during a display dive.

Static Song

Static song is unknown in *S. sasin* (Pitelka 1942, pers. obs.). Static song of *C. anna* is loud and elaborate (spectrographs in Mirsky 1976, Wells et al. 1978, Fig. 3B this study) and may last over 3 sec. The hybrid Anna ×Allen sang its static song in a posture very similar to the Anna Hummingbird, i.e., with body sloped forward and head turning from side to side to flash the gorget. The structure of the hybrid's song (Fig. 3C, D), however, is quite unlike the Anna's and consists of 2 or 3 chip notes 3.5–5.5 kHz in frequency, each chip lasting about 0.02 sec. Each chip was separated from the next by intervals of 0.13–0.37 sec.

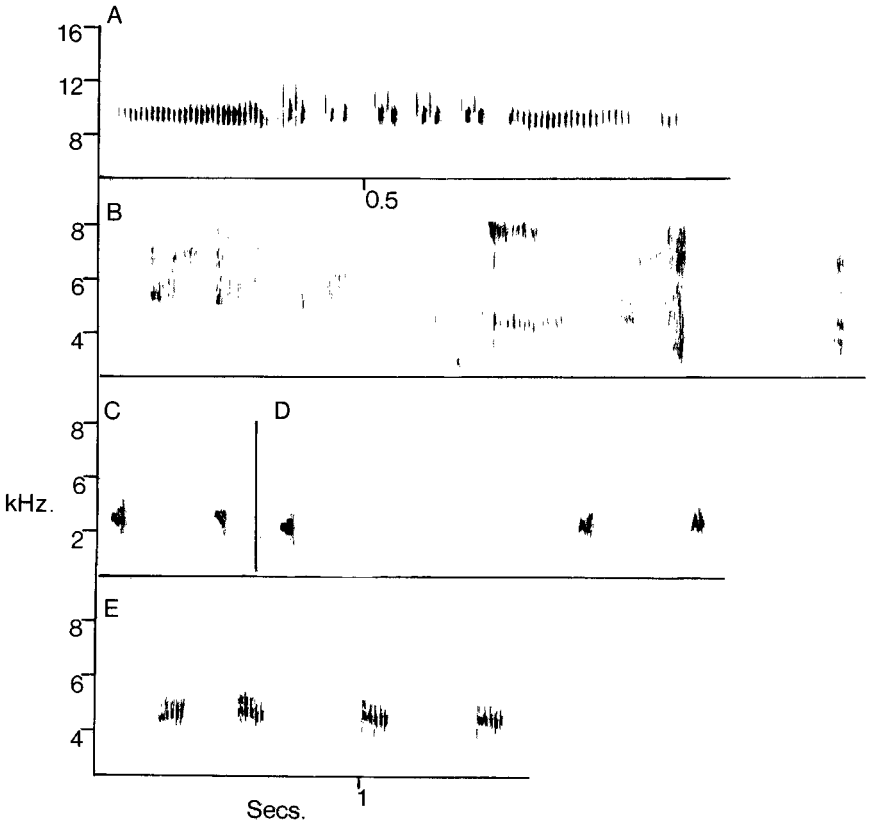

FIG. 3. (A) Twittering noises during pendulum display of *Selasphorus sasin*. (B) Portion of song of *Calypte anna*. (C), (D) Two songs from hybrid Anna × Allen. (E) Song of aberrant *Calypte anna* recorded on the Palos Verdes Peninsula, California on 9 December 1976 (see text).

An aberrant Anna Hummingbird song.—On 19 December 1976, we looked for the Anna × Allen hybrid and found an unbanded male Anna Hummingbird in full adult plumage occupying its territory. This bird sang a song unlike any Anna Hummingbird we have ever encountered (Fig. 3E) and unlike subsong of immature birds. The song was stereotyped and consisted of short trills, each trill being between 3.00–4.00 kHz in frequency and lasting about 0.04 sec. Trills were separated from each other by intervals of 0.07–0.13 sec. Since pitch and duration of trills were similar to pitch and duration of chips of the hybrid's song, we at first thought we were observing the hybrid. We soon learned to distinguish the different

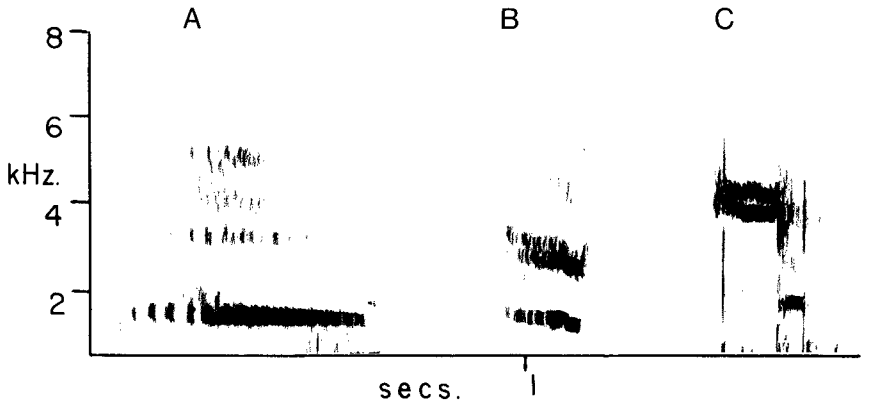

FIG. 4. (A) Sound at the bottom of the nuptial dive of *Selasphorus sasin*; (B) of Anna × Allen hybrid; (C) of *Calypte anna*. Note that the hybrid's sound resembles *Selasphorus sasin*'s in spectral structure, but *Calypte anna*'s in temporal structure.

tonal qualities in their respective songs. Unlike the hybrid, this Anna Hummingbird used its abnormal song in its aerial display.

Song in Anna Hummingbirds may be learned (Mirsky 1976). It is possible that this Anna Hummingbird displaced the hybrid from its territory and learned to produce a poor copy of the hybrid's song during male-male interaction. It is also possible that this apparently "pure" *anna* may have been a backcross to one of the parental forms. The hybrid was nowhere to be seen.

DISCUSSION

Breeding seasons of C. anna and S. sasin sedentarius.—*C. anna* and *S. s. sasin* breed sympatrically from Ventura County to the San Francisco Bay area of northern California (Grinnell and Miller 1944). On the Palos Verdes Peninsula, nests of *C. anna* have fresh eggs or nestlings from 22 December to 26 May (Wells, field notes). Allen Hummingbirds resident on the Palos Verdes Peninsula are referable to the subspecies *sedentarius* (Wells and Baptista, in press), and have been recorded nesting on the peninsula nearly year-round. There is, therefore, much overlap in the breeding season of *C. anna* and *S. s. sedentarius* at Palos Verdes, setting the stage for occasional interspecific hybridization. Wells made frequent observations of male Annas courting female Allens. The introduction of tropical flowering shrubs and trees on the peninsula may have induced Allen Hummingbirds to breed almost circumannually.

It is possible that our hybrid is the product of a mating between a *S. s.*

TABLE 2
FEATURES IN THE DISPLAY OF THE ANNA × ALLEN HYBRID COMPARED WITH THE ANNA AND ALLEN HUMMINGBIRDS

	Anna	Hybrid	Allen
Visual components			
Bill pointed down	+	+	−
Undulatory flight during climb	−	+	+
Pause high in air prior to climb	+	−	−
Pause at top of climb	+	±	−
Pendulum flight before climb	−	−	+
Acoustic components			
Static song display	+	+	−
Song in aerial display	+	−	−
Chirrup sounds during display	−	−	+
Dive sound an interrupted whistle	−	+	+
Dive sound short (±0.07 sec)	+	+	−
Fundamental of dive sound at 1.75 kHz	−	+	+

sasin and a resident *C. anna*. However, bill length of our hybrid is longer than previously reported hybrids and longer than the nominate *sasin*, a strong clue that *S. s. sedentarius* was one of the parents.

Display of the hybrid.—The displays of the hybrid were quite stereotyped in 10 of the 11 features studied (Table 2). The only variable character was the pause in the air at the top of the climb, an *anna* feature that was sometimes absent in the hybrid's display. We can recognize 6 *anna* characters and 5 *sasin* characters in the hybrid's displays (Table 2). The pendulum flight (Fig. 2), so characteristic of *S. sasin* displays, is absent in the hybrid. The structure of the hybrid's song (Fig. 3) resembles neither parent. It is noteworthy that the dive "pop" of the hybrid is similar to *S. sasin* in spectral structure, but more similar to *C. anna* in temporal structure (Fig. 4, Table 2). Hybrid displays contain components similar to both parental forms, intermediate between the 2 parental forms, or resemble neither parental form (review in McGrath et al. 1972, Baptista 1978). Our data indicate that the hybrid hummer's display contained elements from both parents. Its song resembled that of no hummingbird's described to date.

The display of the Anna × Allen hybrid resembles the display of the Anna × Costa Hummingbird (*Calypte costae*) hybrids (Wells et al. 1978) in that (1) the male ascends with head pointed down as in *anna*, and (2) song is absent in the aerial display.

SUMMARY

A hybrid between the Anna Hummingbird (*C. anna*) and Allen Hummingbird (*S. sasin sedentarius*) is described. The dive display of the hybrid shows components from both parental types. The hybrid's song resembles neither parent. Quasi-circumannual breeding has been found for both parental species on the Palos Verdes Peninsula, California, setting the stage for occasional hybridization.

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LITERATURE CITED

BANKS, R. C. AND N. K. JOHNSON. 1961. A review of North American hybrid hummingbirds. Condor 63:3–28.

BAPTISTA, L. F. 1978. Behavior genetics studies with birds. Proc. 1st Intern. Symp. on Captive Birds (Seattle, Washington, 1978) [in press].

BASSETT, F. N. 1921. The nuptial flight of the Allen Hummingbird. Condor 23:37.

COGSWELL, H. L. 1957. Anna's Hummingbird. P. 151 *in* Audubon Western Bird Guide (H. R. Pough, ed.). Doubleday and Co., Inc., Garden City, New York.

GRINNELL, J. AND A. H. MILLER 1944. The distribution of the birds of California. Pac. Coast. Avif. 27:1–608.

MCGRATH, T. A., M. D. SHALTER AND W. M. SCHLEIDT. 1972. Analysis of distress calls of chicken × pheasant hybrids. Nature 237:47–48.

MIRSKY, E. N. 1976. Song divergence in hummingbird and junco populations on Guadalupe Island. Condor 78:230–235.

PEARSON, O. P. 1960. Speed of the Allen Hummingbird while diving. Condor 62:403.

PITELKA, F. A. 1942. Territoriality and related problems in North American hummingbirds. Condor 44:189–204.

RIDGWAY, R. 1911. The birds of North and Middle America. Pt. V. U.S. Nat. Mus. Bull. 50.

WELLS, S., R. BRADLEY AND L. F. BAPTISTA. 1978. Hybridization in *Calypte* hummingbirds. Auk 95:537–549.

——— AND L. F. BAPTISTA. 1979. Breeding of Allen's Hummingbird (*Selasphorus sasin sedentarius*) on the Southern California Mainland. Western Birds (in press).

WILLIAMSON, F. S. L. 1957. Hybrids of Anna and Allen hummingbirds. Condor 59:118–123.

MOORE LAB. ZOOLOGY, OCCIDENTAL COLLEGE, 1600 CAMPUS RD., LOS ANGELES, CALIFORNIA 90041. ACCEPTED 8 NOV. 1978.