COURTSHIP DISPLAYS AND SONATIONS OF A HYBRID MALE BROAD-TAILED × BLACK-CHINNED HUMMINGBIRD

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Abstract. We describe the courtship displays and sonations of a male hybrid Broad-tailed × Black-chinned Hummingbird (Selasphorus platycercus × Archilochus alexandri). The hybrid performed shuttle and dive displays similar to the displays of the parent species. His wing and tail morphology were intermediate between those of the parental species. The hybrid produced dive sounds with rectrix 5 (R5), matching the mechanism of the tail-generated portion of the dive sound of the Black-chinned Hummingbird, and not matching that of the Broad-tailed Hummingbird, which uses rectrix 2 (R2). The hybrid's R2 was capable of fluttering at a frequency and mode similar to those of the Broad-tailed's R2, but unlike the Broad-tailed's R2, the hybrid's R2 produced little sound. During displays, but not during ordinary flight, the hybrid's wing trill was higher pitched than that of either parental species. These results indicate that small changes in feather morphology can result in comparatively large changes in sound production. All of the hybrid's morphological characters and most of the display characters were intermediate between those of the parental species; at least one behavioral character was transgressive, suggesting that some behavioral display characters may be under the control of comparatively few genes.

Key words: Archilochus alexandri, display, hybrid, Selasphorus platycercus, sonation, transgressive.

INTRODUCTION

Hybrids offer insights into the genetic mechanisms underlying the phenotype such as sexually selected characters (Grant and Grant 1994, Phillips 1915, 1921). Individual morphological characters of hybrids tend to be intermediate between those of the parental species, although they may lie closer to one parent than the other (Graves 1990, 2008, Marini and Hackett 2002, Phillips 1915, 1921, Rieseberg et al. 1999, Stelkens and Seehausen 2009). But some characters of hybrids are not intermediate: these non-intermediate characters are termed transgressive characters (Rieseberg et al. 1999, Stelkens and Seehausen 2009). One apparently rare type of transgressive character is the "atavistic" character, which is a character present in the hybrid but absent in both parental species, although it may be present in close relatives. For instance, a hybrid Red Shoveler × Northern Shoveler (Anas platalea × A. clypeata) exhibited atavistic plumage characters on the head and neck found in relatives but not present in either parental species (Harrison and Harrison 1963). The more common type of transgressive character is that in which the character is present in the parents but the hybrid's character state falls outside that of the parents, termed heterosis (Birchler et al. 2010, McCarthy 2006). Heterotic traits...
are common in plants (Rieseberg et al. 1999, Stelkens and See-hausen 2009), but there are fewer examples in animals. As a marginal avian example, Graves (1998, 1999) documented two hybrid hummingbirds (Lesbia victoriae × Chalcostigma herr-anni and Aglaeocercus kingi × Metallura tyriantha) with plumage a bit bluer than that of either parental species. These patterns of character inheritance in hybrids have been better described for morphological characters than for behavioral characters, because many hybrids are only known from museum skins with which behavior or sounds have not been preserved. But stereotyped behavioral characters such as courtship displays can show the same range of patterns (i.e., intermediate, heterotic, atavistic) as morphological characters. In some cases hybrids’ displays are apparently intermediate, such as aspects of courtship displays of Greater × Lesser Prairie-Chicken (Tymanphanus cupido × T. pallicinctus; Crawford 1978), hybrid Sharp-tailed Grouse (Tymanphanus phasianellus) × Greater Prairie-Chicken (Evans 1966), or F₂ M allard × Pintail (Anas platyrhynchos × A. acuta; Sharpe and Johngard 1966). In other cases, hybrids lack any courtship displays, even when given exogenous hormones to induce dis-plays, as Poulsen (1950) did with a hybrid Branta canadensis × Anser alibronis. In ducks of the genus Anas, hybrids can exhibit atavistic displays known in relatives but not found in either parental species (K altenhäuser 1971, Lorenz 1958). Hybrids may also exhibit a combination of intermediate and atavistic behaviors, as found in a Common M erganser × Common Shelduck (Mergus merganser × Tadorna tadorna; Lind and Poulsen 1963) and A nna’s × Costa’s Hummingbird (Calyptra anna × C. costae; Wells et al. 1978). Numerous hybrid combinations have been reported in North America hummingbirds (Banks and Johnson 1961, Graves 2007, Short and Phillips 1966, Wells et al. 1978). Courtship displays are known from two of these: A nna’s × Costa’s (Wells et al. 1978) and A nna’s × A llen’s (Calyptra anna × Selasphorus sasin sedentarius; Wells and Baptista 1979). Here, we describe the displays of a third combination, an adult male Broad-tailed × Black-chinned (S. platycercus × A. alex-andri) — hereafter, “the hybrid” — and examine its phenotype for evidence of transgressive behaviors. This hybrid combina-tion was first described by Banks and Johnson (1961). M ales of species in the “bee” hummingbird clade (Mc Guire et al. 2007) typically perform two types of displays. Display dives are those in which the male ascends meters above the female and then swoops past her at high speed, while shuttle displays are close-range, low-speed displays featuring aerobatic maneuvers and are typically <1 m from the female. Male Broad-tailed and Black-chinned Hummingbirds both make sonations (mechanical sounds with apparent communi-cative function: Bostwick and Prum 2003) during their court-ship displays. However, they do so with different individual wing and tail feathers. The Broad-tailed Hummingbird produces a loud wing trill with an acoustic frequency of ~6.5 kHz with primary 10 (P10; Calder and Calder 1992, Miller and In- ouye 1983) and during its display dive makes a buzzing sound with rectrix 2 (R2) (Clark et al. 2011a), a sound similar to the sound R2 produces in the dives of the Scintillant (Selasphorus scintilla) and Volcano (S. flammula torridus) Hummingbirds (Clark et al. 2011b). During its dives, the Black-chinned Hum-mingbird makes sounds with a different rectrix, R5 (Feo and Clark 2010). It also generates a wing trill with an acoustic frequency typically of 4–5 kHz, possibly with its modified inner primaries, P1–P6 (Stiles et al. 2005), although the mechanism that produces the trill is unclear. To determine how these differ-ent mechanisms of sound production were blended in the hybrid, we tested the sound-production capacity of the tail feathers and P10 of the parental taxa and of the tail feathers of the hybrid in a wind tunnel.

METHODS

Both the Black-chinned and B road-tailed Hummingbirds breed in the inland mountain west of North America. The Black-chinned breeds in mesic and riparian areas that range from shrubby to forested, mainly 0–2000 m above sea level (B altother and R ussell 2000). The Broad-tailed breeds primarily from 2000 to 3000 m above sea level, in alpine and riparian areas adjacent to or interspersed with forests of various types (see Calder and Calder 1992). M ales of both species hold large courtship territories in open areas (meadows, clearings) with a canopy height <3 m, often near riparian areas (Calder and Calder 1992, Feo and Clark 2010). The two species are sympatric at ~2000 m elevation across broad parts of their range. Both species fall within the North America branch of the “bee” hummingbird clade (McGuire et al. 2007).

Feo and Clark (2010) have described the displays of the Black-chinned Hummingbird in detail. The Broad-tailed Hum-mingbird’s displays are poorly described. We obtained sound recordings of two displaying Broad-tailed Hummingbirds in the White Mountains of California in July 2008 (37.5335° N, 118.1482° W; 2800 m above sea level), as well as recordings of dives from one of these birds after we plucked his entire tail. We also obtained sound recordings from three males of the Broad-tailed in the Chisos Mountains of Big Bend National Park, Brew ster County, Texas (29.2482° N, 103.3110° W, 2000 m above sea level) in May 2010 as they displayed naturally or to a mount of a female A nna’s. In addition, we saw and heard multiple dives of roughly ~10 additional males that were not recorded, and we supple-mented our sound recordings with additional recordings from Xeno-Canto (www.xeno-canto.org) and the B orror L aboratory of Bioacoustics (blb.biosci.ohio-state.edu). We were unable to record high-speed videos of Broad-tailed Hummingbird displays.

THE HYBRID

The hybrid was in a canyon in the Ft. Davis Mountains, Davis County, Texas (30.625° N, 104.131° W; 1900 m above
sea level), at a set of 15 hummingbird feeders in a ponderosa pine–oak forest with an understory of pinyon pine, juniper, madrone, and oaks. The canopy was relatively closed (>75% covered). Both Black-chinned and Broad-tailed Hummingbirds were common, breeding in their respective preferred habitats in the general vicinity. The hybrid was originally captured and banded E14593 by Bob and Martha Sargent on 17 August 2006, at which time, in immature plumage, it was misidentified as a hatch-year male Broad-tailed Hummingbird. The hybrid was not detected in 2007, but in March 2008 it was recaptured at the same locality in adult plumage. At this time its status as a hybrid was ascertained on the basis of multiple morphological characters intermediate between the two hypothesized parental species. Other hummingbirds known or suspected to breed locally include the Magnificent (Eugenes fulgens), Broad-billed (Cyanthus latirostris), and White-eared (Hylocharis leucotis) Hummingbirds (Bryan 2008), but the hybrid had no morphological characters suggesting intermediacy with these taxa, and its morphology matched that of a male Black-chinned × Broad-tailed hybrid described by Banks and Johnson (1961; MVZ 136628).

After it was identified as a hybrid in March 2008, it remained in the area and defended a territory encompassing the feeders, in which it attacked or displayed to both male and female Black-chinned and Broad-tailed that attempted to visit the feeders. Males of neither the Black-chinned nor Broad-tailed occupied courtship territories in the immediate area of the feeders, as the habitat was more closed than males of either species prefer for a courtship territory. The hybrid abandoned its territory in early September, when it presumably flew south for the winter. The hybrid reappeared in mid March and repeated this territorial behavior in 2009, 2010, and 2011.

DISPLAY BEHAVIOR
On 20 May 2010, we recorded natural dives that the hybrid performed to other hummingbirds (likely female Black-chinned). We also elicited shuttle displays and dives from the bird with a stuffed mount of a female Archilochus Anna's Hummingbird. His perches were inaccessible so we placed the mount on a feeder. When the hybrid discovered the mount, he performed a long shuttle display, followed by three dives. Later he performed a short shuttle display and one dive, but thereafter ignored the mount. We captured him with a feeder-trap for measurements, photographs, and a sample of tail feathers, then released him.

We recorded the displays’ sounds with a shotgun microphone (Sennheiser M K H70, Old Lyme, CT) connected to a 24-bit digital recorder (Sound Devices 702, Reedsburg, WI) less than 2 m from the mount. We recorded video of the shuttle display at 500 frames sec^-1 by using a color high-speed camera (Miro EX4, Vision Research, 800 x 600 resolution; Wayne, NJ) with an 80–200 mm f/2.8 lens (Nikon, Tokyo, Japan) mounted to the camera with a c-mount to Nikon converter.

WIND-TUNNEL EXPERIMENTS
We tested the hybrid’s R2 and R5 in a wind tunnel to document their sound-producing capabilities, using methods described by Clark et al. (2011a). We also tested tail feathers and wing feathers from a male Broad-tailed Hummingbird and P10 and P9 from a male Black-chinned Hummingbird collected in Big Bend National Park. Briefly, we placed the feathers in the tunnel and adjusted their orientation until they produced sounds similar to the sounds the birds naturally produce (i.e., the feather produced a range of sound frequencies spanning the sounds produced by the wild bird). We tested the feathers over a range of biologically relevant air speeds (generally 15–25 m sec^-1).

We analyzed sound recordings in Raven 1.3 (www.birds.cornell.edu/raven), field recordings with a 512-sample window (Hann, 50% overlap), wind-tunnel recordings with a 65 536-sample window. Videos and sound associated with this research have been deposited in the Macaulay Library (accession ACC2764), and specimens have been deposited at Yale University’s Peabody Museum (accession VZA.00564).

Values reported in the results are means ± SD.

RESULTS
THE HYBRID’S MORPHOLOGY
A male Black-chinned and Broad-tailed Hummingbirds are easy to identify on the basis of their gorget, wing morphology, and tail morphology. The hybrid was intermediate between the Black-chinned and Broad-tailed in all morphological characters considered (Table 1, Figs. 1, 2), including emargination of R2, tapering of R5, and shape of both the outer and inner primaries. The hybrid’s bill was longer than the mean for males of both the Broad-tailed and Black-chinned caught at the same locality (Table 1) but was not significantly different from that for the Black-chinned (t-test, P = 0.2). His gorget was intermediate in color and slightly smaller in size than the Broad-tailed gorget (Fig. 1). As in Archilochus, the feathers directly under the bill were not iridescent, but this dull area was less extensive than the black chin of the Black-chinned Hummingbird and was dark green rather than black.

During ordinary flight, the hybrid produced a quiet but distinctive wing trill with a relatively broad frequency range, at an average acoustic frequency of 6.74 ± 0.54 kHz (range 6.17–7.46; n = 4 recordings), which was not different from that of the trill of the Broad-tailed, 6.33 ± 0.15 kHz (range 6.09–6.59; n = 9 birds). When the hybrid was displaying the wing trill was slightly higher (see below). The hybrid made chip calls and scolding calls during interactions with other hummingbirds. Like both of the parental species, he did not sing.

DISPLAYS
High-speed videos of the hybrid’s shuttle display showed the male flying back and forth laterally (side to side), approximately 10 to 20 cm from the mount (Fig 3; see also Condor online for complete video). We term each lateral motion a “shuttle
TABLE 1. Measurements and morphological characteristics of adult male Black-chinned and Broad-tailed Hummingbirds and the hybrid from the Ft. Davis Mountains, Texas. Values are means ± SD (range). All birds were measured in May or June (mid breeding season), and had no body fat.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Black-chinned (n = 22)</th>
<th>Hybrid</th>
<th>Broad-tailed (n = 17)</th>
<th>Hybrid’s state^a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body mass</td>
<td>3.03 ± 0.20 (2.6 – 3.5)</td>
<td>3.05</td>
<td>3.32 ± 0.30 (2.8 – 3.9)</td>
<td>I</td>
</tr>
<tr>
<td>Wing chord</td>
<td>41.1 ± 1.4 (37.8 – 43.7)</td>
<td>45.1</td>
<td>48.4 ± 0.9 (46.6 – 49.8)</td>
<td>I</td>
</tr>
<tr>
<td>Bill length</td>
<td>17.2 ± 1.0 (15.6 – 19.7)</td>
<td>18.5^b</td>
<td>16.9 ± 0.8 (15.5 – 18.2)</td>
<td>I^b</td>
</tr>
<tr>
<td>Tail length (R 3)</td>
<td>25.6 ± 0.7 (24.5 – 27.0)</td>
<td>30.0</td>
<td>33.1 ± 1.0 (31.0 – 35.0)</td>
<td>I</td>
</tr>
<tr>
<td>Gorget (see Fig. 1)</td>
<td>Small, purple, extensive black chin</td>
<td>Intermediate, pink, small greenish chin</td>
<td>Large, reddish-pink, reaches base of bill (no black chin)</td>
<td>I</td>
</tr>
<tr>
<td>Tail shape (see Fig. 2A)</td>
<td>Tapered R 5</td>
<td>R 2 and R 5 both somewhat tapered</td>
<td>Tapered R 2</td>
<td>I</td>
</tr>
<tr>
<td>Outer primary shape (see Fig. 2B)</td>
<td>P10 curved, not narrowed</td>
<td>P10 straight, somewhat narrowed</td>
<td>P10 recurved, narrowed</td>
<td>I</td>
</tr>
<tr>
<td>Inner primary shape (see Fig. 2B)</td>
<td>P1–P6 have very narrowed outer vane</td>
<td>P1–P6 have somewhat narrowed outer vane</td>
<td>P1–P6 do not have an especially narrowed outer vane</td>
<td>I</td>
</tr>
</tbody>
</table>

^aIntermediate in all characters.
^bNot significantly different from the bill length of the Black-chinned (z-test, P = 0.2).

FIGURE 1. Gorget of (A) Black-chinned Hummingbird, (B) hybrid Black-chinned × Broad-tailed Hummingbird, and (C) Broad-tailed Hummingbird. All photographs taken under similar lighting conditions without any digital processing. (D) The hybrid in flight, showing R 2 and R 5 and the gap between P9 and P10 caused by the narrowed P10. Photographs courtesy A nad Varma.
During the entire display the male's head remained upright and facing the mount despite dramatic variation in wing, body, and tail kinematics. The hybrid kept his bill pointed directly at the mount, and he kept the gorget spread such that the feathers along the margins of the gorget were erected to increase the surface area directed toward the recipient.

The amplitude of the shuttle segments was approximately 0.4 m. At the end of a shuttle segment the male reversed direction. As he re-oriented to accelerate in the opposite direction, the body and tail swept around and the tail was slightly spread. The wingbeat frequency was 67.1 ± 2.4 Hz (n = 10 shuttle segments) during the first half of each shuttle segment as the bird accelerated, then lessened to 60.2 ± 0.8 Hz (n = 9) during the second half of the shuttle segment as his speed decreased (Fig. 3). The overall motion was approximately sinusoidal, with the male continuously in motion, flying back and forth. Each shuttle cycle (1 cycle = 2 segments) took approximately 0.63 sec. Assuming harmonic motion and an amplitude of 0.4 m, his velocity mid-shuttle reached approximately 4 m sec⁻¹, and at the ends of each shuttle segment, accelerations were on the order of 40 m sec⁻². No videos of the shuttle display of either parental species were available for a comparison of the detailed kinematics. The single Broad-tailed shuttle we observed had an amplitude of roughly 0.2 m, in agreement with the description of Calder and Calder (1992).

Shuttle sounds of the Black-chinned, hybrid, and Broad-tailed Hummingbirds are presented in Fig. 4. The sound produced by the hybrid during a shuttle display consisted of a series of buzzy trills. The average trill rate was 64.8 ± 3.4 Hz (Fig. 4; n = 6 syllables from 2 shuttles), equaling the wingbeat frequency during the first part of the shuttle. The average acoustic frequency of the trills was 7.6 ± 0.21 kHz (Fig. 4; n = 2 shuttles), higher pitched than during normal flight.

The hybrid performed bouts of one to three dives; we obtained sound recordings of six dives (Fig. 5). He began the first dive of a bout by ascending with slight whole-body undulations and rapid pulses of wing trill, to a height we estimated to be 30–40 m (above the height of the surrounding pines), then turned and swooped over the mount, tracing out a large U. The bottom of the dive was within 1 m of the mount and passed through the branches of trees. Subsequent dives were in the direction opposite the preceding dive (Fig. 5). The sound produced at the bottom of the dive consisted of a
The trill was relatively broad with an average acoustic frequency of 7.7 ± 0.2 kHz and an average trill rate of 69.6 ± 7.0 Hz (n = 6 dives). The minimum frequency of the tones was 1.8 kHz, and the maximum frequency was 2.2 kHz (n = 6 dives). The average length of each tone was 28 ± 4 msec (n = 18 from 6 dives), and the rate of tone production was 16.2 ± 0.7 Hz.

We obtained one high-speed video of the hybrid as he ascended for a dive. As he rose up and neared the apex of the dive, he briefly stopped flapping twice, the first for 0.12 sec and then for 0.15 sec. Once reaching the top of the dive he flapped weakly during the 0.62 sec spent turning around. In the preliminary stage of descent he resumed flapping with a wingbeat frequency of ~66 Hz, only to cease flapping and hold his wings closed for another 0.15 sec during the descent. After the hybrid resumed flapping, the video lost him against foliage. We observed four dives but were unable to obtain any high-speed videos of the bottom of the hybrid’s dive.

Dives of the Black-chinned Hummingbird, described by Feo and Clark (2010), are depicted in Fig. 5. Briefly, the male ascends approximately 10–15 m, then swoops at a shallow angle over the female, following a U-shaped trajectory. At the end of a dive, the male rotates rapidly and commences another dive in the direction opposite the first dive, and bouts of 5–15 consecutive dives are common. The dive is sometimes performed through or around branches and trees. During the dive, the male Black-chinned alternates flapping his wings with periods of gliding (wings outspread but not flapping) and bounding (wings tucked by sides; see Feo and Clark 2010). The wings produce a trill intermittently during the dive (Fig. 6a), and the male repeatedly spreads and shuts his tail, generating a series of tones (Feo and Clark 2010).

As the males initiated the descent there was a distinctive-sounding preliminary wing trill produced at a relatively slow rate of ~17 Hz, which accelerated as the male descended, so that the trill rate was ~60 Hz (Table 2) at the bottom of the dive. In comparison, the typical wing-trill rate was ~40 Hz during normal flight (Table 2). As in the Black-chinned, subsequent dives were in the direction...
“bleating” sound with a low fundamental frequency (~0.4 kHz) and many harmonics (Fig. 6c) was produced two to four times. This bleating sound was produced at an average rate of 17.9 ± 1.2 Hz (n = 10 dives from 4 males). The bleating sound, but not the wing trill, was absent from the dive-sound of the Broad-tailed that was missing his tail. Though these quantitative observations are of a small sample, we have observed dives by 5–10 additional males that were all qualitatively similar to those described here, suggesting that interindividual variability in this display is slight.

WIND-TUNNEL EXPERIMENTS
Tail feathers from both species and the hybrid fluttered and produced sounds when tested in a wind tunnel. A Broad-tailed Hummingbird’s R2 produced a sound matching the bleating sound made during the dive, a relatively loud sound with a fundamental frequency of 0.3–0.4 kHz and a stack of many integer harmonics (Fig. 7 and online video). A Broad-tailed Hummingbird’s R5 produced faint sounds around 3 kHz unlike any part of that species’ dive-sound. We were able to elicit fluttering from both R2 and R5 of the hybrid (Fig. 7). The tip of the hybrid’s R5 was capable of fluttering and producing a tone with a fundamental of approximately 2 kHz plus harmonics, an acoustic match to the tonal notes of the hybrid’s dive-sound. The tip of the hybrid’s R2, although capable of pronounced fluttering motions at ~0.4 kHz (i.e., matching that of the Broad-tailed’s R2), produced little sound radiated to the microphone, which was ~10 cm from the feather (Fig. 7). As seen in the online high-speed video, the kinematics of the Broad-tailed’s R2 was similar to that of the hybrid with one notable exception. The tip of the Broad-tailed’s R2 oscillated regularly as a unit, with little variation from cycle to cycle. By contrast, when the tip of the hybrid’s R2 fluttered, neighboring barbs in a few parts of the vane had a tendency to detach, and opposite the previous dive. At the bottom of the dive, there were no breaks in the production of the wing trill, suggesting that the wings are flapped continuously during this part of the dive. As the male passed over the female, a second, fainter

FIGURE 4. Spectrograms of shuttle display sounds. (A) Black-chinned Hummingbird with 3 shuttle segments (seg), (B) hybrid with 5 shuttle segments, (C) Broad-tailed Hummingbird with 7 shuttle segments. Wing trill indicated (w).

FIGURE 5. Trajectories of the dives of male Black-chinned and Broad-tailed Hummingbirds and their hybrid, with the approximate dive height and dive width; a, ascent. The Black-chinned ascended for dives flying in a direct line, apparently without undulating or modulating its wingbeat frequency. The hybrid ascended for the first dive of a bout with a slightly undulating trajectory and pulses of wing trill. The Broad-tailed ascended for a dive directly, apparently without undulating, but sometimes stopped flapping momentarily once or twice during the ascent, as indicated by pauses in the wing trill. The preliminary trill of the Broad-tailed’s dive (see Fig. 6) is produced in stage 1, in which the wingbeat frequency is ~17 Hz. The wing trill is elevated to 60 Hz in stage 2 and remains at this frequency during the rest of the dive. Tail sounds are produced in stage 3.
the fluttering of the feather seemed more erratic or chaotic. Recordings of these feathers fluttering are in the online video.

We were unable to get the tip of a Black-chinned’s P10 to flutter and produce sound at air speeds of 15–25 m sec⁻¹, although at these speeds the feather’s trailing vane produced sounds at 5 to 6 kHz. On a live bird this mode of flutter would likely be inhibited by overlap with P9. Over this range of air speeds, the tip of P9 fluttered at approximately 2 kHz, producing sound at both this fundamental frequency and the second harmonic at 4 kHz (Fig. 8), and thus is also not a good match to the wing trill. The tip of a Broad-tailed’s P10 generated sound at 6.5 kHz (Fig. 8), matching that species’ wing-trill, whereas a P9 produced sound at around 4 kHz (Fig. 8). Wing feathers from the hybrid were not available for wind-tunnel tests.

**CHARACTERS OF THE HYBRID WITH RESPECT TO THE PARENTAL SPECIES**

We investigated nine morphological characters (Table 1, Figs. 1, 2), all of which were intermediate between (or, in the case of bill length, not significantly greater than) those of the parental species. All of the hybrid’s morphological characters were similar to those Banks and Johnson’s (1961) described for another male of this hybrid combination. Of 12 flight or behavioral characters (excluding sonations), one or possibly two were transgressive (pulsed wing trill with whole-body undulations during ascent for first dive, and possibly dive height), with the ascent behavior potentially an atavistic character (Table 2). The remaining flight/behavioral characters were clearly intermediate (Table 2). With respect to sonations, the hybrid’s sounds were not intermediate, despite intermediate wing and tail feather morphology (Figs. 1, 2). The pitch of the wing trill matched that of the Broad-tailed during ordinary flight and exceeded it during the shuttle display (Table 2, Fig. 4). The tail-generated portion of the hybrid’s dive-sound was produced only by R5, which matched the Black-chinned, and not the Broad-tailed, which produces sound with R2. By contrast, the wing trill of the hybrid may have been produced by P10 (as in the Broad-tailed), although we were unable to test this rigorously.

**DISCUSSION**

Rarely documented hybrids such as the Black-chinned × Broad-tailed Hummingbird we describe here are both fascinating and frustrating study subjects. As our observations are from a single individual, our conclusions are necessarily limited in their generality, as we do not have any estimate of the interindividual variability of the traits in question. Behaviors are also more challenging than morphology to quantify (both of the parents and the hybrid) — we have been unable to obtain video of shuttle displays of either parental species. With these limitations in mind, we offer the following analysis of the character states exhibited by our single hybrid.

The hybrid’s morphological phenotype consisted of characters intermediate between (or not different from) those of the parents, as seen in other hybrid hummingbirds (Banks and Johnson 1961, Graves 1990, 1997, Graves and Newfield 1996, Wells and Baptista 1979). This suggests that the morphological characters considered (except perhaps bill length) are under the control of a relatively large number of genes that each make small, additive contributions to the phenotype (Graves 1990).

The hybrid’s behavioral phenotype may have been more variable than its morphology. The display behaviors did not closely resemble those of only one of the parental species to the exclusion of the other parent, suggesting that the display behaviors are not learned from a tutor. Instead the display behaviors were mixed, some of which more strongly resembled the Black-chinned’s, some the Broad-tailed’s. Others were intermediate between the two parental species’ behaviors, and at least one behavioral characteristic was transgressive (Table 2, Figs. 4-6).
The transgressive behavior was the bird's audibly flapping its wings in pulses while undulating the trajectory while ascending for the first dive (Table 2, Fig. 5). We and others have observed this behavior in the majority of the related species we have studied, including the Scintillant, Volcano (Clark et al. 2011b), Allen's (Mitchell 2000, Wells and Baptista 1979), Calliope (Stellula calliope), and Costa's Hummingbirds, along with some woodstars (Clark, pers. obs.; Fig. 8), but we have not observed this behavior in any display of the Black-chinned (hundreds of dives by >20 males) or Broad-tailed (dozens of dives by ~15 males), which suggests it is an atavistic behavior. It is possible that we missed observing it in the parental species, as the undulations can be subtle, may precede only the first dive of a bout (rather than preceding all dives), and we started watching specifically for this behavior after most of our observations of the parent species. However, if it is present in either of the parents, it is either expressed so rarely that we have not recorded it, or else the behavior is sufficiently subtle that it does not result in audible pulses of the wing trill in a sound recording. Under either of these possibilities we still interpret the expression of this behavior in the hybrid as transgressive, but as heterotic rather than atavistic.

The other, less conclusive character was dive height. Our estimate of the hybrid's dive height (35 m) was greater than for the Broad-tailed (30 m) or Black-chinned (15 m). There is uncertainty in our estimates of dive height in the Broad-tailed, which is a single general estimate derived from watching multiple displays by multiple individuals. We do not have a measure of intraspecific variation in dive height, although we believe it to be on the order of ~2 meters. As a result, we cannot rule out that the hybrid's dive height was not different from the Broad-tailed's dive height.

The pattern seen here is similar to that reported for hybrid Anna's × Costa's Hummingbirds described by Wells

<table>
<thead>
<tr>
<th>Behavior</th>
<th>Black-chinned</th>
<th>Hybrid</th>
<th>Broad-tailed</th>
<th>Hybrid state</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole-body undulations and rapid pulses of wing trill during ascent for 1st dive</td>
<td>no</td>
<td>yes</td>
<td>no</td>
<td>T</td>
</tr>
<tr>
<td>Dive height (m)</td>
<td>10–15b</td>
<td>35</td>
<td>30</td>
<td>I or T*</td>
</tr>
<tr>
<td>Dive height:width</td>
<td>&lt;1</td>
<td>-1</td>
<td>&gt;1</td>
<td>I</td>
</tr>
<tr>
<td>Typical number of dives per bout</td>
<td>5–15b</td>
<td>1–3</td>
<td>1–4</td>
<td>I</td>
</tr>
<tr>
<td>Number of tail spreads</td>
<td>5–9b</td>
<td>6–7 (6)</td>
<td>2–4 (4)</td>
<td>I</td>
</tr>
<tr>
<td>Tail spread rate (Hz)</td>
<td>13.6 ± 0.8</td>
<td>16.2 ± 0.7 (6)</td>
<td>17.8 ± 1.2 (4)</td>
<td>I</td>
</tr>
<tr>
<td>Glides at bottom of dive</td>
<td>yesb</td>
<td>no</td>
<td>no (4)</td>
<td>I</td>
</tr>
<tr>
<td>Preliminary dive trill rate (Hz)</td>
<td>84.4 ± 4.4</td>
<td>66 (1)</td>
<td>16.9 ± 0.5 (4)</td>
<td>I</td>
</tr>
<tr>
<td>Wingbeat frequency at bottom of dive (Hz)</td>
<td>82.0 ± 4.5b</td>
<td>69 ± 8 (6)</td>
<td>59 ± 1.6 (4)</td>
<td>I</td>
</tr>
<tr>
<td>Shuttle segment frequency (Hz)</td>
<td>1.9b,cd</td>
<td>3.1 ± 0.19 (2)</td>
<td>5.34 ± 0.91 (2)</td>
<td>I</td>
</tr>
<tr>
<td>Shuttle wing trill rate (Hz)</td>
<td>87b</td>
<td>65 (2)</td>
<td>47.5 (2)</td>
<td>I</td>
</tr>
<tr>
<td>Wing trill pitch during displays (kHz)</td>
<td>4 – 5b</td>
<td>7.49; range</td>
<td>6.77; range</td>
<td>I*</td>
</tr>
<tr>
<td>Wing trill produced by</td>
<td>P1–P6?</td>
<td>P10*</td>
<td>P10</td>
<td>*</td>
</tr>
<tr>
<td>Rectrix that produces dive sound</td>
<td>R5</td>
<td>R5</td>
<td>R2</td>
<td>*</td>
</tr>
<tr>
<td>Hovering wingbeat frequency (Hz)</td>
<td>54b</td>
<td>52.1f</td>
<td>–40g</td>
<td>I</td>
</tr>
</tbody>
</table>

*I, intermediate; T, transgressive; *see Discussion.

1From Feo and Clark (2010).
2From high-speed video; the hybrid’s preliminary trill was inaudible.
3From corrigendum to Feo and Clark (2010).
4Wing feathers not tested in wind tunnel to test this hypothesis.
5From high-speed video.
6A Littler (2006) reported a wingbeat frequency of 38 during hovering; sound recordings from wild males in this study suggest a frequency of 43.1 Hz (n = 3 birds), albeit at an unknown flight speed.

The transgressive behavior was the bird's audibly flapping its wings in pulses while undulating the trajectory while ascending for the first dive (Table 2, Fig. 5). We and others have observed this behavior in the majority of the related species we have studied, including the Scintillant, Volcano (Clark et al. 2011b), Allen's (Mitchell 2000, Wells and Baptista 1979), Calliope (Stellula calliope), and Costa's Hummingbirds, along with some woodstars (Clark, pers. obs.; Fig. 8), but we have not observed this behavior in any display of the Black-chinned (hundreds of dives by >20 males) or Broad-tailed (dozens of dives by ~15 males), which suggests it is an atavistic behavior. It is possible that we missed observing it in the parental species, as the undulations can be subtle, may precede only the first dive of a bout (rather than preceding all dives), and we started watching specifically for this behavior after most of our observations of the parent species. However, if it is present in either of the parents, it is either expressed so rarely that we have not recorded it, or else the behavior is sufficiently subtle that it does not result in audible pulses of the wing trill in a sound recording. Under either of these possibilities we still interpret the expression of this behavior in the hybrid as transgressive, but as heterotic rather than atavistic.

The other, less conclusive character was dive height. Our estimate of the hybrid's dive height (35 m) was greater than for the Broad-tailed (30 m) or Black-chinned (15 m). There is uncertainty in our estimates of dive height in the Broad-tailed, which is a single general estimate derived from watching multiple displays by multiple individuals. We do not have a measure of intraspecific variation in dive height, although we believe it to be on the order of ~2 meters. As a result, we cannot rule out that the hybrid's dive height was not different from the Broad-tailed's dive height.

The pattern seen here is similar to that reported for hybrid Anna's × Costa's Hummingbirds described by Wells.
Their hybrids were intermediate in all morphological characters and most behavioral characters examined, but they exhibited an atavistic behavior of flying in horizontal circles between dives, a behavior absent in both parental species, though present in the related Vervain Hummingbird (Mellisuga minima; Clark 2006; Fig. 8). At least one of the behavioral characters we studied in the Black-chinned × Broad-tailed were transgressive, whereas none of the morphological characters were (Tables 1, 2). This pattern suggests that some individual courtship behaviors may be under the control of relatively few genes. This hypothesis would account for the greater variance because individual genes may have large effects individually or through epistasis. This possibility could be examined quantitatively through a study of F₂ hybrids, as in Lorenz’s (1958) and Sharpe and Johnsgard’s (1966) studies of ducks.

**THE HYBRID’S SONATIONS**

The acoustic characters of the hybrid have several implications for how changes in feather shape influence sonations. First, the sonations we observed differ greatly from those produced by the A nna’s × Costa’s hybrid described by Wells et al. (1978). Both Anna’s and Costa’s produce dive sounds with the same part of R₂ (the trailing vane), and both feathers flutter...
in essentially the same transverse mode (Clark et al. 2011a), so A nna’s × Costa’s hybrids use the same feather to produce sounds at a frequency intermediate between those of the parents (Fig. 5C in Clark and Feo 2010).

By contrast, the Black-chinned’s dive sound is made with the tapered tip of R5 (Feo and Clark 2010), whereas the Broad-tailed’s is made with the tapered tip of R2 (Fig. 2A). The hybrid’s tail-feather shapes were intermediate, both R2 and R5 being tapered (Fig. 2A). When the tail is spread during the dive, we predict the tips of both feathers should be isolated from neighboring feathers and thus allow each to potentially flutter and produce sound (Feo and Clark 2010). However, it appears that in vivo only the hybrid’s R5 produced sound (Fig. 6). Our wind-tunnel experiments revealed that even though the hybrid’s R2 could flutter at a frequency and amplitude similar to those of the Broad-tailed’s R2, the mode of flutter did not produce a similar pattern of radiated sound (Fig. 7 and online video). Qualitatively, the barbs of the feather appeared to detach more readily than in the Broad-tailed’s R2, and the resulting fluttering motion seemed somewhat unstable and chaotic. Detaching the barbs from each other is one effective way to silence a feather, and re-attaching them recovers the ability to produce sound (Clark and Feo 2008). This result indicates that there is not a necessarily a 1:1 correspondence between feather shape and sound production. Specifically, there are likely morphological thresholds for the production of a significant amount of sound, such that small changes in the feather’s underlying shape can result in abrupt changes in the mode of flutter that can be excited in a feather, as well as whether that mode generates much sound.

Our results support the hypothesis that P10 generates the wing trill of the Broad-tailed Hummingbird (Fig. 7; Miller and Inouye 1983), whereas we failed to recreate the wing trill of the Black-chinned with its P10. The mechanism that produces the wing trill in the Black-chinned is unclear. The likeliest possibility is the inner primaries, P1–P6, which have narrowed distal vanes (Fig. 2) and Stiles et al. (2005) hypothesized were responsible for the wing trill. How this works is not apparent, however. Possibly sound is produced during displays if this shape allows gaps to appear between these feathers. Sharp high-speed video of the wings during the shuttle display may reveal the mechanism. Regardless of these uncertainties, our data indicate that the two parental species produce their respective wing trills with different feathers. The hybrid appeared to only produce one wing trill, which we suspect was made by P10, because the tip of P10 was clearly narrowed so that a gap appeared between it and P9 during flight (Fig. 1). If this hypothesis is correct, then the hybrid’s wing and tail mechanisms for producing sound each matched a different parental species.

Also notable was the loudness of the hybrid’s displays. Both the wing trill and the dive sound of the hybrid did not seem as loud as the homologous sounds produced by either parental species (Figs. 4, 6). Provided that natural selection has tuned the exact shape of the outer primaries both for a particular pitch, and production of a relatively loud sound, intermediate morphology may fail to be as efficient at radiating sound.

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LITERATURE CITED


