SOUNDS AND COURTSHIP DISPLAYS OF THE PERUVIAN SHEARTAIL, CHILEAN WOODSTAR, OASIS HUMMINGBIRD, AND A HYBRID MALE PERUVIAN SHEARTAIL × CHILEAN WOODSTAR

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Abstract. We describe the songs and courtship displays of three closely related hummingbirds, the Peruvian Sheartail (Thaumastura cora), Oasis Hummingbird (Rhodopis vespert), and the endangered Chilean Woodstar (Eulidia yarrellii). The Peruvian Sheartail and Oasis Hummingbird sing complex multisyllabic songs, while the Chilean Woodstar’s song is monosyllabic and simple. Like North American “bee” hummingbirds (within the tribe Mellisugini), the Chilean Woodstar and Oasis Hummingbird perform stereotypical close-range shuttle displays and larger display dives. The Peruvian Sheartail also performs shuttle and dive displays but their kinematics are variable and they are less distinct from each other. The greatly elongated tail of the Peruvian Sheartail is split widely during display, such that the five rectrices (R1–R5), including R1 and R2 of each side of the tail, project laterally, apparently as a visual signal. Like most other “bee” hummingbirds, all three species produce sounds during their display dives with their three outer rectrices, R3, R4, and/or R5, although the Peruvian Sheartail’s sound is both faint and not produced exclusively during displays. We diagnose an adult male hybrid Peruvian Sheartail × Chilean Woodstar and describe its songs and displays. The hybrid had unique tail morphology with an elongated R2, R3, and R4, and both R1 and R4 were transgressive, longer than those of either parent species. The hybrid was from the Azapa valley, where the Peruvian Sheartail is now common and the Chilean Woodstar rare; hybridization may represent an Allee effect arising from the recent crash of the Chilean Woodstar’s population.

Key words: courtship display, Eulidia yarrellii, hummingbird, hybrid, Rhodopis vespert, sonation, Thaumastura cora.

Sonidos y Despliegues de Cortejo de Thaumastura cora, Eulidia yarrellii, Rhodopis vespert y de un Macho Híbrido Thaumastura cora × Eulidia yarrellii

Resumen. Describimos los cantos y los despliegues de cortejo de tres picafloros cercanamente emparentados, Thaumastura cora, Rhodopis vespert y la especie en peligro Eulidia yarrellii. T. cora y R. vespert cantan canciones multisilábicas complejas, mientras que la canción de E. yarrellii es monosilábica y simple. Del mismo modo que los picafloros “abeja” de América del Norte (dentro de la tribu Mellisugini), E. yarrellii y R. vespert realizaron despliegues estereotípicos de lanzadera de corto alcance e inmersiones de despliegue mayores. T. cora también realiza despliegues de lanzadera e inmersiones pero su cinemática es variable y son menos distintas unas de otras. La gran cola alargada de T. cora se abre enormemente durante el despliegue, de modo que las cinco rectrices (R1–R5), incluyendo R1 y R2 de cada lado de la cola, se proyectan lateralmente, aparentemente como una señal visual. Como la mayoría de los otros picafloros “abeja,” las tres especies producen sonidos durante sus despliegues de inmersión con sus tres rectrices externas, R3, R4 y/o R5, aunque el sonido de T. cora es débil y no se produce exclusivamente durante los despliegues. Diagnosticamos un macho adulto híbrido de T. cora × E. yarrellii y describimos sus cantos y despliegues. El híbrido presentó una morfología de la cola única con R2, R3 y R4 alargadas, y ambas R1 y R4 fueron transgresivas, más largas que las de sus especies de origen. El híbrido proviene del valle de Azapa, donde T. cora es ahora común y E. yarrellii es rara; la hibridación puede representar un efecto Allee que surge de la drástica reducción reciente de la población de E. yarrellii.
INTRODUCTION

The “bee” hummingbirds (tribe Mellisugini) comprise a monophyletic North American clade, which includes the genera *Selasphorus*, *Calypte*, *Archilochus* and relatives, and a monophyletic South American clade. This South American clade includes the Chilean Woodstar (*Eulidia yarrellii*), Peruvian Sheartail (*Thaumastura cora*), and Oasis Hummingbird (*Rhodopsis vesper*), as well as *Chaetocercus* and other woodstars (McGuire et al. 2007, 2009; McGuire, pers comm). Members of the Mellisugini have distinctive tail morphology: all species except *Atthis* spp. are sexually dimorphic, and the male’s rectrices are narrowed, stiffened, curved, tapered, notched, elongated, and/or otherwise unusual in shape (Clark 2010). The tail is the primary taxonomic character used to identify species in this clade (e.g., Graves 1986, Ridgway 1892) and in comparison to other hummingbirds, rate of evolution of tail morphology is greater in the bee hummingbirds (Clark 2010). Our recent work has revealed a functional explanation for all of this diversity: males of the North American clade produce species-specific sounds with the tail during courtship display dives, in which the male passes by the female at high speed (Clark et al. 2011, Clark and Feo 2008). Many North American species also perform close-range “shuttle” displays to the female, in which sounds may be produced by the wings.

There are no detailed descriptions of similar displays by the South American bee hummingbirds. For instance, the only description of the Peruvian Sheartail’s displays is from Baron (1897): “the male is often seen with the tail spread so that the two longest feathers form a nearly straight line, and thus flutters before the female, which may be sitting in a small bush. The male also flies... high up in the air and then comes down swiftly, making a noise with the tail like a ribbon in a strong wind.” As the tail morphology of the South American bee hummingbirds is equally distinctive as that of their North American sisters, we hypothesized that they have homologous displays and also produce sounds with their distinctive tail feathers, such as R2 of the Peruvian Sheartail. Here, we describe the courtship displays and songs of three closely related (van Dongen et al. 2012) sympatric South American bee hummingbirds: the Oasis Hummingbird, Peruvian Sheartail and Chilean Woodstar. We also provide information on the breeding behavior of all three species that may be of value in the efforts to conserve the Chilean Woodstar.

All three species live in the Atacama Desert of far northern Chile and southern Peru. Although the desert receives virtually no precipitation, seasonally flowing rivers support strips of vegetation along the valleys that bisect it, which include (from north to south) the valleys Tacna, Lluta, Azapa, Vítor, and Camarones. Within these small islands of habitat, the hummingbirds of the Atacama breed. The Oasis Hummingbird and Peruvian Sheartail have ranges that extend through the Sechura Desert of coastal Peru, whereas the Chilean Woodstar is an Atacama endemic.

The Chilean Woodstar is endangered (Estades and Aguirre 2010), and if current trends continue, will likely soon qualify as critically endangered, while the Peruvian Sheartail and Oasis Hummingbird have a conservation status of least concern. Historically the Chilean Woodstar was present in Tacna and common from Lluta through Camarones (Estades et al. 2007). Its range has recently contracted southward: it is apparently no longer present in the northern valleys of Lluta or Tacna and is nearly extirpated in Azapa, while it is still present at isolated localities in the southern valleys of Vítor and Camarones (Estades and Aguirre 2010). The decline of the Chilean Woodstar over the past 40 years has been concurrent with two other events (Estades et al. 2007). First, agriculture has replaced most of the native vegetation within its range. Second, the Peruvian Sheartail was historically not present in Chile (Johnson 1972) but has recently expanded its range south, apparently facilitated by the spread of agriculture. It is now common in Azapa, as well as present in small numbers in Vítor and Camarones (van Dongen et al. 2013). Plausible reasons for the cause(s) of the decline of the Chilean Woodstar include habitat loss, competition and/or hybridization with the Peruvian Sheartail, and susceptibility to pesticides (Estades et al. 2007), as well as interactions between these factors, which are not mutually exclusive.

No hybrids involving the Oasis Hummingbird, Peruvian Sheartail, or Chilean Woodstar have been described (McCarty 2006), though many intergeneric hybrids of related taxa have been reported (Banks and Johnson 1961, Graves 1990, 2007, Short and Phillips 1966). Avian hybrids generally exhibit plumage and courtship display behaviors intermediate between those of the parents (Graves 1990), although some characters may match those of a parent species, and a few instances of transgressive display behaviors are known (Clark et al. 2012, Wells et al. 1978). Here, we describe and diagnose the morphology, behavior, and sounds of the first known hybrid Peruvian Sheartail × Chilean Woodstar.

METHODS

This project was approved by the Institutional Animal Care and Use Committee of Yale University and the Ethics Committee of the Faculty of Sciences, Universidad de Chile. Peruvian Sheartails and Oasis Hummingbirds were captured and collected under permit 3731 from the Servicio Agrícola y Ganadero of Chile (SAG) to CJC. WvD captured Chilean Woodstars under SAG permits 5163 and 3291.

We observed the three species of hummingbirds from 17 September through 3 October 2010 in the Azapa and Vítor valleys, Region XV, Chile. The three main localities of our study were at the bridge on highway I-5 over the Rio Vítor, in the Chaca region of Vítor (18.802° S, 70.171° W), hereafter “Puente Chaca,” 1 km south of km post 24 of highway A-27, east of Arica in Valle Azapa (18.566° S, 70.088° W), hereafter
“km 24,” and km post 33 of highway A-27, east of Arica in Valle Azapa (18.581° S, 69.998° W), hereafter “km 33.” Immediately upstream of Puente Chaca was an acre or so of somewhat undisturbed native vegetation, including an extensive thicket along the bottom of the wash with a canopy up to 10 m high. We observed all three species at this locality and obtained recordings of five male Chilean Woodstars on a lek. Km 24 was a decrepit olive plantation in which we obtained recordings of all three species. It consisted of a small olive orchard and a few small patches of thick bushes and trees on the south side of the wash of Rio Azapa. It was surrounded by farms. Km 33 was an open area between the highway and the wash of Rio Azapa, with sparse scattered low bushes surrounded by fields, wash, and barren desert. A significant component of the vegetation was the bush Tecoma fulva, which was in bloom. We obtained recordings of Peruvian Sheartails and Oasis Hummingbirds at this locality.

DATA COLLECTION

Sound recordings of songs and displays were recorded with a shotgun microphone (Sennheiser MKH 70, Sennheiser Corp., Old Lyme, CT) attached to a 24-bit digital recorder (Sound Devices 702, Reedsburg, WI), often within a few meters of the subject. High-speed video of courtship displays was obtained with a color high-speed camera at 500 frames per second at 800 × 600 pixels (Miro EX4, Vision Research, Wayne, NJ). Additional video recordings of displays were made with an HD Sony handicam HDR-SR12 at 30 frames per second.

Males of all three species defended distinct territories and spent most of their time perched on a few specific perches. Undirected song (i.e., vocalizations produced in the apparent absence of a receiver) was recorded from males singing spontaneously from these song perches. We observed few natural courtship displays of the Peruvian Sheartail and none of the Oasis Hummingbird. We elicited courtship displays and directed song of these two species by placing a conspecific female in a cage on a male’s territory. In contrast, our recordings of Chilean Woodstars were almost exclusively of natural displays; a single display was elicited with a caged female Peruvian Sheartail.

We collected tail feathers from the Peruvian Sheartail and Oasis Hummingbird for wind-tunnel tests of whether these feathers could produce sounds similar to those generated by the wild birds. Specimens of these two taxa were also collected, and photos were taken of caged Peruvian Sheartails and Oasis Hummingbirds. No specimens or feathers of the Chilean Woodstar were taken, nor were the birds caged; all captured Chilean Woodstars were released within a few minutes of capture.

THE HYBRID

On 29 September at km 24, we detected a new hummingbird defending a space between two previously identified territories, one of a male Chilean Woodstar and the other of a Peruvian Sheartail. It was obvious, and we had not detected it previously, suggesting that the bird appeared at km 24 on the afternoon of 28 September or the morning of 29 September. We placed a caged female Peruvian Sheartail on the male’s territory, which elicited four dives and then no further displays; no videos were obtained. At about 16:00 the same day the male was captured. Measurements and recordings indicated it could not be a Chilean Woodstar, so it was photographed and collected (Yale Peabody Museum [YPM] 142233). We compared it side by side with specimens at the American Museum of Natural History (AMNH), though the specimens of the Chilean Woodstar there are discolored (as reported by Graves 1986). For color, we compared YPM 142233 to photos of live birds.

WIND-TUNNEL ANALYSES

We tested three sets of tail feathers of the Peruvian Sheartail (R2 through R5) and Oasis Hummingbird (R3 through R5) in a wind tunnel to determine whether they could produce sounds similar to those recorded during display dives. Each feather was mounted individually in the approximate orientation of a tail spread 180° and tested at speeds that bracket possible dive speeds. A full description of the methods is presented elsewhere (Clark et al. 2013). Here, we present the frequency that each feather produced as a function of airspeed, in order to determine which feather(s) are candidates for production of the dive sound.

SOUND AND VIDEO ANALYSES

We assembled kinematic descriptions of dive sequences by comparing the high-speed videos of dives, supplemented with standard videos and visual observations. Sample sizes for specific kinematic events vary according to the subset of videos that reveal the event in question. We analyzed sounds in Raven 1.3 (birds.cornell.edu/raven) and measured up to six recordings per male and computed an average for that individual. Specimens were deposited in the Yale Peabody Museum of Natural History (YPM), and sounds and video were deposited in the Macaulay Library at the Cornell lab of Ornithology (accession ACC2764). Means are presented ± SD.

RESULTS

PERUVIAN SHEARTAIL

Males were observed at all three field sites, but most of our recordings are from km 33, where males were abundant. A given male held a territory incorporating 5–10 exposed perches, often dead twigs at the top of a bush, or on a telephone wire, 2–5 (occasionally 10) m in height. Many territories spanned sparsely scattered bushes 2–3 m in height, although some were in small thickets up to roughly 5 m in height and thick enough to be difficult to walk around. The core area bounded by males’ perches was approximately 40 m × 40 m with neighboring
CHILEAN HUMMINGBIRD DISPLAYS

Territories abutting so that some neighboring males perched within 10 m of each other. Nearly all territories had food, blooming *T. fulva*, which was ubiquitous in Azapa, and had a long corolla matching the shape of Oasis Hummingbird’s bill (Altshuler and Clark 2003). Peruvian Sheartails accessed these flowers with their short bills through slits cut in the corolla by the Cinereous Conebill (*Conirostrum cinereum*). All 23 flowers on which we observed sheartails feeding had a slit, while in a random sample of 60 flowers only 68% had conebill slits. Sheartails also occasionally fed from *Plucrea chingoyo* and *Trixis cacalooides*, which were less abundant.

Territorial males were active and rarely perched for more than a few minutes. Often up to four males, presumably neighbors, vigorously harassed and chased each other for several minutes, while stridently singing continuously. Once, the chases involved several males pursuing, “floating” (see below), and displaying to a female, interspersed with additional chases between the males. At km 33 we rarely observed female Peruvian Sheartails near males’ territories. Typically we detected a female through a male’s frenzied behavior, subsequently spotting her hidden deep inside of a bush. Females seemed to favor areas with greater canopy cover, i.e., orchards.

**Sounds.** Male Peruvian Sheartails produced songs that were not obviously directed at another individual, as well as for females during and between displays. The song was rambling and squeaky and consisted of at least four syllable types (a–d in Fig. 1A), normally strung together in long sequences. Syllable d, a sharp, dry *chit*, was frequently uttered in long repeated sequences between more rambling parts of the song. Syllable a was uttered only in directed song produced during displays. Males often repeated the same sequence of syllables (i.e., phrase) in their own songs, but it appeared that different males’ phrases varied. During agonistic interactions with other males, in which other bee hummingbirds produce a distinct “scolding” call, male Peruvian Sheartails produced vocalizations with syllables similar to those of the song (Fig. 1C). Other vocalizations included short, dry “chip” calls with unknown function, produced spontaneously by females.

Peruvian Sheartails did not have a notable wing trill. During courtship displays, and sometimes during ordinary flight, whining sounds were produced. This sound was always produced when the male had his tail spread during forward flight (Fig. 1D). Because of its apparent homology with the tail-generated dive sounds of many of its relatives, we call it a dive sound, although

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**FIGURE 1.** Sounds produced by males of the Peruvian Sheartail (*Thaumastura cora*). (A) Part of a song, which was a rambling series of four syllable types, labeled a–d. Syllable order (and possibly syllable types) varied from individual to individual. (B) Sounds of part of a shuttle display, which consisted of song (syllables not labeled) and pulses of wing hum (wh) that became loud (arrows) and faint as the male flew back and forth, approaching and moving away from the microphone. (C) Agonistic interaction between two males; “grunts” apparently given by submissive bird. Scolding calls contained components similar to syllables c and d of the song. (D) Dive sound, showing multiple nonharmonic frequencies; arrow indicates lowest frequency. (E) Sounds produced by isolated R3, R4, and R5 in a wind tunnel at an airspeed of 11.7 m sec⁻¹. Fundamental frequency indicated with arrow, although not visible for R3. Second and third integer harmonics of sound are also labeled.
it was not produced exclusively during dives. During displays the dive sound had a duration of 0.42 ± 0.07 sec (n = 6). It consisted of multiple tones, the lowest of which had a frequency of 0.80 ± 0.06 kHz (n = 6). It was similar in pitch to the sound that R3 produced in the wind tunnel (Table 1, Fig. 1E). Additional frequencies were usually present that were not integer harmonics and were slightly higher pitched than the lowest frequency (Fig. 1D). These sounds may have been produced by R4 and/or R5 (Table 1, Fig. 1E), which in the wind tunnel produced tones that were slightly higher than those generated by R3. This whining sound was somewhat accentuated during the undulating portion of a dive. We tested two undamaged R2s at airspeeds of approximately 10 m sec\(^{-1}\); both fluttered wildly at low frequency and produced little sound. The sounds that R3, R4, and R5 produced were all generated by fluttering of the feather’s tip.

### Displays
Males frequently performed a behavior we term “floating,” in which they hovered, stationary, 1 to 10 m above vegetation on their territory. The wingbeat frequency during floating was 69 ± 5.5 Hz (n = 3 videos), well above the typical hovering wingbeat frequency (Table 2). With bill pointed down a male turned its head from side to side, hovering in place for up to a couple of minutes. The apparent function was a search for a visiting female or intruder in the vegetation below. Many related species also perform this behavior (CJC, pers obs.), and it normally terminates with either the male locating and interacting with the bird it was searching for, or apparently failing to locate the other bird and flying to a perch. In other species the male may descend while hovering but remains above the canopy. This behavior was unique in the Peruvian Sheartail in that, while scanning, males slowly descended down through

### Table 1

<table>
<thead>
<tr>
<th>Species and feather</th>
<th>Frequency (kHz)</th>
<th>Critical velocity (m sec(^{-1}))</th>
<th>Dive sound (lowest) (kHz)</th>
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</thead>
<tbody>
<tr>
<td><strong>Peruvian Sheartail</strong></td>
<td></td>
<td></td>
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<tr>
<td>R5</td>
<td>1.61 ± 0.34 (3)</td>
<td>9.5 ± 0</td>
<td>0.80 ± 0.06 (6)</td>
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<tr>
<td>R4</td>
<td>1.17 ± 0.20 (3)</td>
<td>7.6 ± 0.4</td>
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<tr>
<td>R3</td>
<td>0.78 ± 0.13 (3)</td>
<td>6.6 ± 1.6</td>
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<tr>
<td><strong>Oasis Hummingbird</strong></td>
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<tr>
<td>R5</td>
<td>0.38 ± 0.14 (3)</td>
<td>9.5 ± 3.2</td>
<td></td>
</tr>
<tr>
<td>R4</td>
<td>0.30 ± 0.08 (2)(^a)</td>
<td>8.8 ± 1.0</td>
<td>0.72 ± 0.14 (5)</td>
</tr>
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<td>R3</td>
<td>0.55 ± 0.07 (3)</td>
<td>10.0 ± 0.4</td>
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</table>

\(^a\) A third R4 of an Oasis Hummingbird produced sound at 2.4 kHz, omitted from mean.

### Table 2

<table>
<thead>
<tr>
<th></th>
<th>Oasis Hummingbird</th>
<th>Peruvian Sheartail</th>
<th>Hybrid</th>
<th>Chilean Woodstar (^a)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Male (14)</td>
<td>Female (10)</td>
<td>Male (6)</td>
<td>Male (1)</td>
</tr>
<tr>
<td>Body mass (g)(^b)</td>
<td>4.6 ± 0.2</td>
<td>5.0 ± 0.3</td>
<td>2.5 ± 0.2 [2.3–2.8] (19)</td>
<td>2.45</td>
</tr>
<tr>
<td>Wing chord (mm)</td>
<td>53.6 ± 1.0</td>
<td>55.5 ± 1.9</td>
<td>38.8 ± 0.9 [37.5–40.8] (19)</td>
<td>37.2</td>
</tr>
<tr>
<td>Exposed culmen (\text{mm})</td>
<td>28.9 ± 2.0</td>
<td>31.0 ± 1.0</td>
<td>16.4 ± 0.5 [15.6–17.5] (19)</td>
<td>15.2</td>
</tr>
<tr>
<td>R1 (mm)</td>
<td>20.5 ± 1.0</td>
<td>28.2 ± 1.1</td>
<td>13.7 ± 1.2 [12.0–15.4] (19)</td>
<td>17.6</td>
</tr>
<tr>
<td>R2 (mm)</td>
<td>29.0 ± 1.2</td>
<td>33.7 ± 1.2</td>
<td>89.8 ± 0.7 [75.5–97.2] (19)</td>
<td>42.8</td>
</tr>
<tr>
<td>R3 (mm)</td>
<td>40.1 ± 1.3</td>
<td>35.1 ± 0.9</td>
<td>45.4 ± 5.2 [33.6–55.6] (19)</td>
<td>45.1</td>
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<tr>
<td>R4 (mm)</td>
<td>47.9 ± 1.6</td>
<td>34.2 ± 0.8</td>
<td>33.0 ± 3.2 [25.9–37.9] (19)</td>
<td>41.3</td>
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<td>R5 (mm)</td>
<td>49.6 ± 2.0</td>
<td>31.7 ± 1.2</td>
<td>24.5 ± 1.8 [20.4–28.0] (19)</td>
<td>22.1 ± 1.4</td>
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<tr>
<td>Hovering wingbeat frequency (Hz)(^c)</td>
<td>36 ± 2.4 (5)</td>
<td>32 ± 2.0 (6)</td>
<td>49 ± 4.6 (9)</td>
<td>42 ± 2.7 (5)</td>
</tr>
</tbody>
</table>

\(^a\) From van Dongen et al. (2013).
\(^b\) Gravid females excluded.
\(^c\) From high-speed video.
the canopy of a bush, sometimes to within a few decimeters of the ground, suggesting that the male was searching for the target hummingbird deep inside the bush. Both times we saw a male naturally displaying to a female, the female was perched deep inside the bush, close to the ground.

Many male Peruvian Sheartails responded frenetically to the stimulus of a caged female placed in a bush. Sometimes they seemed unaware of the female’s exact location and performed the “floating” behavior in the bush near or underneath the cage (i.e., looking for the female below her actual location). Some males performed long bouts of displays to the female (occasionally >30 min) and ended their displays only after additional males began to intrude onto the focal male’s territory to look at or also display to the female in the cage. When this occurred the focal male focused on evicting the other male(s), and performed few additional displays.

Courtship displays typically began with the male hovering above the female with an elevated wingbeat frequency, singing. After a bout of song the male transitioned to a series of repeated flights back and forth past the female. As a part of these displays, the male spread the gorget, maximizing the surface area directed towards the recipient, and held the tail spread widely.

These back-and-forth flight displays of the Peruvian Sheartail were less stereotyped than the distinct shuttle and dive displays of other related bee hummingbirds. The display flights seemed bimodal, with both relatively large display dives (Fig. 2A–D) and relatively small shuttle displays (Fig. 2E–G). In contrast to those of the other species, the kinematics of the two displays overlapped (particularly in the amplitude of the flights), and a few displays were ambiguous. It appeared that males sang vigorously during the smaller displays (shuttles), and did not sing during the larger displays.

**FIGURE 2.** Kinematics of the courtship displays of the Peruvian Sheartail (Thaumastura cora). (A–D) Dive displays; (E–G) shuttle displays. (A–B) Two dives filmed from a similar oblique angle, showing a dive with (A) and without (B) undulations. Images are 1/30 sec apart. Dives were performed to a female in a cage (bottom right of frame). See also Fig. 4C–D for additional depictions of similar undulations. (C–D) Sketch of dive trajectory in the vertical (C) and horizontal (D) planes. Males ascended 0 to 10 m and then rapidly turned and descended, swooping past the bush in which the female was perched. The tail was widely spread through this entire flight. Females typically perched near the bottom of the bush. After passing over the female, males sometimes engaged in undulating flight as indicated. (D) Horizontal projection of trajectory of two dives. First dive (D1) is depicted by a solid line. After performing this dive, the male performed a second dive. Either he turned and dove in the direction opposite the previous dive (dashed line D2a) or he curved the trajectory around so that the subsequent dive (D2b) was 90° relative to the first dive, in the horizontal plane. (E) Composite of a male performing one shuttle segment to a caged female, in which he flew in a line past the female, then turned. During the shuttle the male kept the tail spread 180° and remained facing the female. The amplitude of each shuttle segment varied from 0.5 to 2 m. (F) Male performing a shuttle display. The tail, including the R1s (arrows), was widely spread throughout the shuttle display. (G) Sketch of male performing five shuttle segments (numbered) to a female in a cage. The male typically flew back and forth along the same path (segments 1–3), but occasionally switched directions (transition from 3 to 4), shuttling along a new line (4–5).
displayed sounds (dives), so we have divided the behavior into these two categories by the presence or absence of song. However, males often switched back and forth between performing bouts of shuttle and dive displays. Individuals varied greatly in their propensity to shuttle or dive, with some primarily shuttling and some primarily diving, although all individuals performed both types of displays. Examples of the dives and shuttles are presented in a video available at http://dx.doi.org/10.1525/cond.2013.120047, as well as at www.youtube.com/watch?v=M8DeiswDB8k.

“Dives” were back-and-forth flights performed by the male that were usually larger in amplitude than the shuttle. Not stereotyped, they ranged in horizontal amplitude from 1 to 15 m. The male ascended vertically 0 to 10 m, then turned and swooped past the female at relatively high speed, describing a shallow J (Fig. 2A–C). Occasionally the male did not ascend; these “dives” were simply fast horizontal flights past the female. Dives usually passed within 1 m of the female.

The wings were typically flapped throughout the dive at 75 ± 3.5 Hz (n = 8 males), but occasionally the male briefly glided when approaching or passing over the female. The tail was kept spread at roughly 180º throughout the dive, and the tips of R2 visibly fluttered in aerodynamic response to each wing beat. Occasionally the male undulated the forward trajectory of the dive just after passing over the female (Fig. 2A, B). High-speed video suggested that these undulations were produced by the male rolling to one side, in a fashion similar to the Oasis Hummingbird (see below). Males often performed bouts of dives, with subsequent dives either in the direction opposite the previous dive or at a 90º angle (azimuth) from the previous dive. In the latter, at the end of a dive the male looped around to the right or left and then dove again, so that the two subsequent dives traced out a figure 8 in the horizontal plane, with the female near the intersection (Fig. 2D).

Shuttles consisted of a series of flights back and forth past the female along a curving or straight line that tended to be short, ranging in amplitude from 0.5 to 2 m (Fig. 2E–G). Each short flight we term a “shuttle segment.” At the end of a shuttle segment the male changed direction. Often the male reversed direction and flew back the way he had come, returning him to his initial position after two shuttle segments (Fig. 2G). Occasionally the male flew in a new direction, causing the orientation of the display to shift, as from one face of the cage holding the female to another (Fig. 2G). The males rotated their bodies to remain facing the female as they passed by. During this display the wingbeat frequency was 73 ± 8.3 Hz (n = 7 males), and shuttle segments were performed at a frequency of 1.8 ± 0.3 Hz (n = 5 males).

The tail was spread 180º throughout this display. Of note, high-speed videos and photos clearly indicated that the R1s were widely split, such that they projected laterally out to either side of the bird, rather than posteriorly (Fig. 2F). Many individuals had R2s that were damaged, but in those in which the feathers were intact, the combination of the black R5, R4, and R3 contrasted with the white on R2 and gave a striking impression of a black-on-white stripe protruding laterally from each side of the bird (Fig. 2F).

**OASIS HUMMINGBIRD**

Male Oasis Hummingbirds held territories at all three localities. We recorded displays of four individuals at km 33 and of two at km 24. The males spent most of the day perched on roughly 5–10 locations (typically dead twigs) at the tops of the trees or bushes, or on telephone wires 2–15 m high, in an area of roughly 40 × 40 m. Territories tended to include some relatively tall or thick bushes, and most in Azapa had blooming *Tecoma fulva*. In some instances there was complete overlap with territories of male Peruvian Sheartails. Elsewhere we saw male Oasis Hummingbirds evict male Peruvian Sheartails from their territories. Males’ territories tended to be widely dispersed, with nearest neighbors often >100 m apart, though sometimes neighboring territories were as close as 50 m apart. Females and young birds foraged and nested in between males’ territories.

**Sounds.** Males sang a quiet, undirected song from their territorial perches. The song included a series of short syllables sung rapidly with frequent repetitions of the same syllable (Fig. 3A). Four syllables have been labeled a–d in Fig. 3A, and there may be additional syllable types not identified. One syllable, labeled “d,” was frequently repeated many times in a row, as was syllable “d” of the Peruvian Sheartail’s song. This syllable was also uttered during other behaviors such as dives (Fig. 3C).

Wing sounds and song were produced during the shuttle display (Fig. 3B). The dive sound consisted of a raspy tone repeated in pulses that coincided with the undulating motions at the bottom of the dive (Fig. 3C, D). The sound produced by five of the six recorded males consisted of a tone of 0.72 ± 0.14 kHz (n = 5) and up to three integer harmonics. The initial pulse (p1 in Fig. 3C) was the longest and produced during stage 2 of the dive (see below), as the male passed over the female, and had a duration of 0.34 ± 0.12 sec (n = 5). Subsequent pulses (p2, p3 in Fig. 3C) were produced during stage 3 of the dive. In the wind tunnel, R3, R4, and R5 all produced sound in which the feather tip bent and fluttered in the airflow. The frequencies produced by the three feathers ranged from 0.3 to 0.6 kHz (Table 1), increased slightly with increasing airspeed, and included prominent integer harmonics. The closest match to the dive sound appeared to be the sounds produced by R5 (specifically its even harmonics), and of the three feathers this was also the one that produced the loudest and most consistent sounds in the wind tunnel.

**Atypical male.** One male that we recorded and then collected (YPM 141931) had the plumage and behavior of an adult male except that he had retained three juvenile rectrices (left R4, right R4, R5) through an incomplete molt. This male's
The dive sound was not clearly different from that of the other five males we recorded; the fundamental tone of his dives was $0.59 \pm 0.03$ kHz with a duration of $0.27 \pm 0.047$ sec ($n = 6$ dives). The timbre of his dive sound was somewhat distinctive, but as the timbre of the other five males’ sounds also varied, the conservative conclusion is that this male’s dive sounds fell within this range of variation. We were unable to determine if the other five males we recorded all had adult tail morphology.

Displays. We obtained recordings from six males of two types of stereotypical displays performed to caged females. The initial display was a shuttle display. The males approached within 10 or 15 cm of the female, flared the gorget and sang while hovering, slightly jerking up, down, and side to side with accentuated, atonal wing sounds (Fig. 4A). High-speed video revealed the males were not flapping continuously but rather were “bounding” in place—the wings were intermittently folded by the sides for $0.067 \pm 0.007$ sec ($n = 3$ birds), followed by the next pulse of flapping. The frequency of the bounding was $4.3 \pm 0.19$ Hz, and the birds’ wingbeat frequency (excluding bounds) was $54 \pm 2.0$ Hz ($n = 3$), higher than the hovering wingbeat frequency (Table 2). The tail was also widely spread and flipped out to one side or the other (and not necessarily alternating sides), at somewhat irregular intervals (Fig. 4A).

After performing one to several bouts of shuttling (perching and singing between bouts), the males performed bouts of one to four dives. We observed roughly 50 dives total by six males, and we obtained 11 high-speed videos of four males (one to five dives per male). The male ascended for a dive at approximately a 45° angle while flipping the widely spread tail from side to side and slightly waggling the trajectory (Fig. 4B), traveling roughly 15 to 20 m vertically and 20 m horizontally. Occasionally while waggling during ascent the males made sounds similar to the dive sound.

The dive had three stages. In stage 1, the male descended toward the female at a roughly 45° angle. He then pulled up, passing within 5 m of the female. As a male passed over the female (stage 2), he rolled (i.e., rotated about his longitudinal axis) and/or spread the tail once, without undulating. He then transitioned to stage 3, in which he executed a series of undulating motions while performing additional rolls (Fig. 4D, E). The
FIGURE 4. Shuttle and dive displays performed by males of the Oasis Hummingbird. (A) Frames from a high-speed video of a shuttle display. Time (sec) in lower left of each frame. The shuttle display consists of a jerky hovering in which the male periodically flips the tail to either side (a) or momentarily folds the wings by the sides (b). The sequence of behaviors (a) and (b) did not always alternate; either (a) or (b) could be performed multiple times successively. (B) Trajectory of shuttle display (dashed line). In some of the cycles of tail flipping and wing tucking, the male flew laterally, apparently to maintain position in front of the female, but the cyclical back-and-forth flights characterizing shuttle displays of most close relatives are lacking in this species. During the display the male simultaneously sang and produced faint buzzing sounds with the wings (see Fig. 3). (C–E) Dive display of the Oasis Hummingbird. (C) Dive trajectory in a vertical plane. The male ascended for the dive with a slightly undulating trajectory while flipping the widely spread tail from side to side. After rising 10 to 15 m, he turned and dove in a shallow “J” over the female. In the first stage of the dive (1), the male descended by gliding. In stage two (2), the male began flapping and spread the tail one or more times. After passing over the female, the male began stage 3, in which he performed a series of undulations. (D) Dive trajectory in the horizontal plane. After performing the undulations of the first dive (D1), the male curved horizontally, flying along the circumference of an enormous circle around the female. In some instances, the male flew 90° of this circle, so that the second dive (D2a) was 90° relative to the first dive (D1). In other instances, the male flew 180° around the circle, so that the second dive (D2b) followed the same trajectory as the previous dive. (E) Frames from a high-speed video of a dive, showing part of stage 2 and stage 3 from an oblique angle (“cam” in C indicates camera orientation). Each frame is 0.02 sec apart. In stage 2, the male flew right side up. To undulate, the male rotated (rolled) until upside down (arrows), then rolled in the opposite direction until upside down again, then rolled in the opposite direction again.
male, starting from a roll angle of 0° (i.e., right side up, flying forward), rolled 180° to one side (i.e., rotating about his longitudinal axis until he was upside down and continuing to travel forward) with a spiraling forward trajectory (arrows in Fig. 4E), then reversed and rolled in the opposite direction until he was right side up again, thus completing the first undulation. The next undulation was performed as the male continued the rolling motion until he was again upside down, then reversed the direction of rotation yet again. These undulations were performed roughly six to eight times (Fig. 4D), during which the male flew approximately 20 m horizontally, away from the female.

The males’ wing kinematics varied slightly from dive to dive. Although they generally flapped their wings at 54 ± 2.7 Hz (n = 4 males) through the dive, they occasionally stopped flapping to bound (wings tucked at sides) or glide (wings outspread but not flapping). This sometimes occurred during stage 1 of the dive as the male descended or as the male started the first undulation (i.e., transition from stage 2 to 3).

The male’s tail was clearly spread widely late during stage 2 and during stage 3, and in particular the tail was widely spread during each undulation, while the male was upside down. It was not possible to determine from the videos how many times the tail was spread and shut, or the duration of the spreads, as the tail was at times obscured by the rolling motions in all the videos we obtained. The undulations coincided with the pulses of dive sound (Fig. 3C).

After performing a dive (which was approximately 40 m, horizontal), the male flew in a large circle while ascending for the next dive (Fig. 4C). A male flew either 180° of the circumference of this circle, so that the second dive followed a trajectory similar to that of the first, or he flew 90° of the circle and then dove, so that the two dives traced a horizontal figure 8 with the female at the intersection (Fig. 4C). The third dive then followed the trajectory of the first dive, in a fashion similar to some Peruvian Sheartail dive sequences (Fig. 2C). After the last dive of a bout, the male performed the undulating flight into the distance (i.e., not turning or returning to the female), apparently flying to one of his distant territorial perches.

A minority of the bouts were initiated as the male hovered by the caged female, then abruptly accelerated directly away while performing the undulations (including production of the tonal dive sound), i.e., essentially performing stage 3 of the dive from rest. The male then proceeded to perform additional dives as in Fig. 4C.

CHILEAN WOODSTAR

Five adult male Chilean Woodstars held territories at Puente Chaca, two more at km 24. All seven territories were over dense tangles of bushes and short trees 3 to 10 m high, and most lacked any type of flower. The males perched 3–10 m high, often on bare exposed branches in the crowns of the tallest trees in the territory, and the perches enclosed an area of roughly 20 × 20 m. One to three perches were favored, although roughly five more were occasionally used. All five territories at Puente Chaca and the two at km 24 were clustered with the centers of neighboring territories 50 m apart. Males often left their territories to chase or display to neighboring males. The males at Puente Chaca occasionally flew in the direction of a large, undefended patch of blooming chañar (Geoffroea decorticans) nearly 200 m distant.

Sounds. We did not detect differences in sounds between the two populations, so results for the seven males have been pooled. The song of the Chilean Woodstar was short and relatively simple (Fig. 5A), a high-pitched trill lasting about half a second, spanning a frequency of about 7 to 11 kHz, and a trill rate of 69.8 ± 4.9 Hz. Males broadcast this sound from their territories in the apparent absence of a receiver, and females did not produce it. The males sang often: from their perches, when flying to or from the territory, while performing the dive display, and when chasing other hummingbirds (typically other male Chilean Woodstars clustered with the centers of neighboring territories 50 m apart. Males often left their territories to chase or display to neighboring males. The males at Puente Chaca occasionally flew in the direction of a large, undefended patch of blooming chañar (Geoffroea decorticans) nearly 200 m distant.

**FIGURE 5.** Sounds produced by males of the Chilean Woodstar (Eulidia yarrellii). (A) Song, which consisted of a single syllable, a trill with a frequency range spanning 7 to 11 kHz and a rate of 69.8 ± 4.9 Hz. (B) Scolding call given by one male chasing another. Similar to song (note that the scaling of the x axis differs), except multiple syllables were often given in sequence (five syllables labeled), and scolding calls often slurred downward in frequency, especially evident in syllable 3. (C) Dive sound, including two vocal trills and the tones, which are produced during stage 2 of the dive by the outer tail feathers (See Fig. 6A–C). (D) Sounds produced by the wings during the shuttle display, which consisted of a buzzy trill and claps. One shuttle segment and one cycle are indicated, corresponding to the kinematics shown in Fig. 6D.
but also Oasis Hummingbirds and Peruvian Sheartails). The song had many similarities to a wing trill (e.g., of Broad-tailed Hummingbird, *Selasphorus platycercus*) such as its pitch, timbre, cadence, and the timing of production during flight. During agonistic interactions with other males, males also uttered “scolding” calls (Fig. 5B), which were similar to song except that multiple syllables were strung together (Fig. 5B) and individual syllables descended slightly in pitch.

The sound produced during the dive consisted of a song followed by a sound produced as the tail was spread and shut (Fig. 5C). The loudest portion of this sound was a pair of high-pitched trilled tones; the higher tone had an average pitch of $10.4 \pm 0.43$ kHz, the lower one of $9.4 \pm 0.45$ kHz ($n = 7$). There was also a quieter broadband-frequency component to the sound (Fig. 5B), and the entire sound was repeated at a rate of $41.2 \pm 2.2$ Hz ($n = 7$), matching the rate of tail spreading. The sound produced during the shuttle display was a high-pitched metallic buzzing and consisted of two types of sounds that we termed trills and claps (Fig. 5D).

**Displays.** Male Chilean Woodstars performed stereotyped display dives (Fig. 6A–C). They sometimes dove to passerine birds or other males but most often to female Chilean Woodstars. The dive traced a broad U in a vertical plane, approximately 20 m horizontal and 20 m vertical (Fig. 6C). After a dive the males sometimes floated above the vegetation for up to 2 min.

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**FIGURE 6.** Courtship displays of the Chilean Woodstar (*Eulidia yarrellii*). (A) Composite image from a high-speed video of a natural dive. In stage 1 of the dive, the male descended with a shut tail. In stage 2, the male rapidly spread and shut the tail while producing a high-pitched trill (see Fig. 5C). In stage 3, the male ceased spreading the tail and ascended. The wings were always flapped continuously though stages 1 and 2, and often through stage 3 as well. (B) Stage 2 in more detail. The tail is spread to approximately 180º, then repeatedly briefly shut and then spread again. (C) Sketch of the dive trajectory. The males ascended without undulations to a height of roughly 20 m above the object of display, and sometimes floated at the apex, prior to a dive (see text). The trajectory of the dive was a broad U, always without undulations and in a vertical plane. In most cases, at the end of the dive, the males rose up to their start height. Subsequent dives were usually in the direction opposite the previous dive. (D) Two composite images of successive segments of a shuttle display, from a high-speed video. During the display, the male flew back and forth along a horizontal line roughly 1 m long, with gorget spread, facing the object of display at all times. Wing sounds produced during this display are shown in Fig. 5C. Images are 0.04 sec apart. The shuttle was directed at a gall (arrow, G), with which this male false-copulated on multiple occasions. During the display the tail was often widely spread (e.g., times 0.12, 0.72), and as the male passed by the recipient in the middle of each shuttle segment, the widely spread tail was rapidly pumped up and down several times.
Subsequent dives traced the reverse of the previous dive, unless
the female switched location. Bouts of approximately 15 dives
were common (range 1–28).

High-speed videos of four males revealed three stages to
the dive (Fig. 6A). Initially the male descended on flapping
wings (stage 1). Then at the bottom of the dive, as he passed over
the recipient, he rapidly spread and shut the tail 6 to 10 times
(stage 2), at a rate of 40 ± 1.7 Hz (n = 7 videos of 2 males)
(Fig. 6B). In this stage, the tail was spread 180° for 75% of
the cycle, i.e., it was shut only momentarily between each
spread. He then ceased tail spreading and ascended (stage 3).
The wings were flapped continuously at a rate of 85.9 ± 3.7
Hz (n = 6 males) during stages 1 and 2; during stage 3 the
males sometimes continued continuous flapping or sometimes
briefly glided or bounded. In at least one instance, a male per-
formed an aborted dive: midway through stage 2 he abruptly
slowed, turned, flew straight to the female, and started a shut-
tle display.

The males often performed stereotyped shuttle displays
to male and female Chilean Woodstars, other hummingbirds,
passerines, or a hummingbird-sized leaf or clump of fruit
near a territorial perch. Four males were observed shuttle-
isplaying to such inanimate objects, and three appeared to
false-copulate with the object at the end of the shuttle. The
shuttle display consisted of rapid back and forth lateral flights
(shuttle segments) approximately 1 m in amplitude, in which
the male faced the object of display continuously (Fig. 6D).
We obtained three high-speed videos of shuttles from each
of two males. During each shuttle segment the male held the
tail widely spread and rapidly depressed and raised it as he
passed by the recipient over the first part of each shuttle seg-
ment (Fig. 6D). The wingbeat frequency was 92 ± 1.6 Hz
(n = 2 males) during the first half of each segment as the
male accelerated, then briefly decreased to 69 ± 2.6 Hz at the
end of each segment, during deceleration. The shuttle-cycle
frequency (where 1 cycle = 2 segments) was 1.02 ± 0.13 Hz
(n = 6 males). The wing trill (Fig. 5D) was produced at a rate
of 92.8 ± 0.8 Hz (n = 6), matching the wingbeat frequency
during the first half of each segment, while the claps were
produced at a rate of 44.3 ± 1.5 Hz (n = 6). How these sounds
are produced by the wings was not evident from the high-
speed video.

Male–female interactions. One male Chilean Woodstar at
Puente Chaca received multiple visits by one or more females
each of the mornings that we watched him, and we observed
several long natural display sequences. The female perched rel-
atively prominently, often near one of the male’s perches. The
male flew to within a few centimeters of the female, who spread
her tail and responded by (1) sitting still, (2) flying to another
perch, or (3) flying straight at the male with her tail spread. If
the female flew at the male, he ascended and performed 1 to 15
dives. The male passed within 1 m of the female at the bottom
of the dive. If the female switched perches while the male was
diving, he adjusted the location of his dives to her new location
or paused the display and floated (see above). After diving the
male flew to the female and started a shuttle display, and the
female then responded with one of her three behaviors. These
interactions typically lasted 1 to 5 min. These interactions once
ended in copulation: after a few minutes of performing bouts of
dives and shuttles, the male performed a relatively long shuttle
display, then mounted the female for a few seconds. After copu-
lation, he launched into another bout of dives, and the female
left the territory shortly thereafter.

DIAGNOSIS OF THE HYBRID
We considered the hypotheses that YPM 142233 is any combi-
nation of the Peruvian Sheartail, Oasis Hummingbird, and
Chilean Woodstar. We discounted two species found in
nearby habitats, the Sparkling Violetear (Colibri coruscans)
and Giant Hummingbird (Patagona gigas), on account of size.
YPM 142233’s complete gorget, song, aggressive behavior,
lack of corrugations on the rhamphotheca, and enlarged testes
identified it as an adult male in breeding condition (Yanega
et al. 1997). He had just finished gorget molt, as a line of white
malar feathers overlaying fully grown gorget feathers, obvi-
ous in pre-capture photos, fell off during capture.

Morphological measurements of each species are provided
in Table 2. YPM 142233 is intermediate between the Chilean
Woodstar and Peruvian Sheartail in most of the morphological
characters considered (Fig. 7, Table 2). Male Chilean Wood-
stars have the elongated R3, R4, and R5 attenuated distally and
no white in any of the rectrices (Fig. 7), and a rectrix-length
formula of R5 ≈ R4 ≈ R3 > R2 > R1. Male Peruvian Sheartails,
by contrast, have a formula of R2 >> R3 > R4 > R5 > R1, a
pattern unique within hummingbirds (Clark 2010), along with
extensive white in the R2 (Figs. 2F, 7). YPM 142233 has a
formula of R2 ≈ R3 > R4 > R5 > R1, in which R2 is only
slightly longer than R3 or R4 and has some white in the lateral
vane (Fig. 7A). At the level of individual rectrices, R1 and R4
are transgressive (Table 2). In aggregate, his rectrices appear
to be intermediate between one parent with a greatly elongated
R2 (Peruvian Sheartail), and another with an elongated R3, R4,
and R5 (Chilean Woodstar). We conclude that YPM 142233 is a
hybrid Peruvian Sheartail × Chilean Woodstar. Behavioral and
acoustic characters presented below, as well as genetic analyses
(van Dongen et al. 2013), also support this determination.

The hybrid’s behaviors and displays. When discovered,
the hybrid appeared to be establishing a territory at the edge
of an olive orchard, in a patch of trees 5–10 m tall, and spent
most of his time on three perches within an area of 20 × 20 m,
immediately adjacent to the thicker habitat containing the
two male Chilean Woodstars. His songs were more com-
plex than the Chilean Woodstar’s songs, comprising at least
two repeated syllables (labeled buzz and notes) sung multiple
times in succession (Fig. 8A). The buzz phrase was similar
to the Chilean Woodstar’s song, consisting of a trill with a
frequency range of 7 to 11 kHz and a pulse rate of $88.5 \pm 5.9$ Hz ($n = 6$ phrases), always immediately followed by two or three notes. During agonistic interactions with male Chilean Woodstars (Fig. 8B) and during dives (Fig. 8C) he also made an apparent scolding call that was distinct from the song and similar to some syllables from the Peruvian Sheartail’s song. He performed one shuttle display to a hummingbird-sized clump of fruit. The shuttle sound was faint but similar to that of a Chilean Woodstar’s shuttle and consisted of a wing trill with a frequency of about 8 kHz and pulse rate of 96.1 Hz. The shuttle-cycle frequency was approximately 1 Hz (Fig. 8D). He did not sing while shuttling.

The hybrid male displayed once to a caged female Peruvian Sheartail. He initially floated beneath the cage with his bill pointed down, apparently scanning for the female near the bottom of the foliage, like a floating Peruvian Sheartail. When he located the female he performed one bout of four dives. We detected no sounds that were likely produced by the tail, but during two of the four dives, he produced scolding calls (Fig. 8C) after passing over the female. Later he performed another bout of at least three dives to an unidentified recipient. The dives were approximately 5 m horizontally and 2 m vertically (Fig. 9). All of the dives had similar kinematics, and subsequent dives were in the direction opposite that of the previous dive. That is, they resembled the Chilean Woodstar’s dives in shape but the Peruvian Sheartail’s in size (Fig. 9). We glimpsed the widely spread tail at the bottom of the dive but were uncertain whether the tail was held spread or if it was rapidly spread and shut. None of the display behaviors were clearly transgressive (Table 3).
DISCUSSION

The displays described here appear to be homologs to those of the North American clade of bee hummingbirds: each species performed dives consisting of repeated gravity-powered flights past the object of display and a close-range shuttle display in which the gorget is spread and the male beats his wings in pulses of greatly elevated frequency, interspersed with periods of flapping at a lower frequency. The Oasis Hummingbird’s shuttle was extreme in this respect, in that the male ceased flapping altogether between the pulses of high-frequency flapping. The distinctive undulations in some dives of the Peruvian Sheartail (Fig. 2) and all dives of the Oasis Hummingbird (Fig. 4) recur in the dives of many other woodstars (e.g., Chaetocercus spp.; CJC, unpubl. data), as well as those of basal North American bee hummingbirds (e.g., Diaz-Valenzuela et al. 2011, Scott 1994). This behavior was also expressed in other contexts: in the Oasis Hummingbird, we observed that males occasionally initiated displays by undulating away from a female, starting from rest, and some hummingbirds outside the tribe Mellisugini (e.g., Chlorostilbon ricordii) perform similar undulating flights in an aggressive context (CJC, pers obs.). This behavioral component of the dive may be ancestral in the bee hummingbird clade.

As these displays are produced ardently by males for females during the breeding season, we infer that they are under sexual selection. Sexually selected morphology is often more variable than other morphological characters (e.g., Alatalo et al. 1988), an apparent paradox, as directional selection by female preferences should depress genetic variation. Whether sexually selected behaviors show a pattern similar to that of morphology has not been demonstrated. The kinematics of the Peruvian Sheartail’s displays were more variable than those of any other bee hummingbird we have studied (e.g., Clark and Feo 2008, Feo and Clark 2010). It may be that only specific elements of the display are targets of female preference, so the wide variation we observed is the result of relaxed selection on some aspects of the displays, such as dive height. The tail also appears to be a visual signal (Fig. 2F) during display, not the case in the Peruvian Sheartail’s sister taxa.

Like the bee hummingbirds of the North American clade, all three species studied here apparently produced
distinctive dive sounds with the tail feathers. Our wind-tunnel tests revealed that the outer tail feathers of the Oasis Hummingbird and Peruvian Sheartail flutter and generate sound. The aerodynamic response of the isolated R3, R4, and R5 of both species were all broadly similar, in that the distal portion of the feather bent and oscillated in moving air (Clark et al. 2011).

In the Oasis Hummingbird the feather most important for the sound seemed to be R5, as this was the feather that produced the loudest sounds in the wind tunnel, and the even harmonics (2nd, 4th, etc.) of the sound produced in the wind tunnel were similar to the dive sound. R4 and/or R3 may play a role in sound production, through their interactions (Clark et al. 2011). Our sound recordings of the male Oasis Hummingbird (YPM 141931) that retained both juvenile R4’s and one R5 into adulthood, though somewhat distinctive, were not outside of the variation in the recordings of five adults. This individual’s ability to produce a dive sound is consistent with our hypothesis that R5 is principally responsible for this species’ dive sound, as this male had one adult R5. We hypothesize that he made sound with only half of his tail, so his dive sound may have been fainter than that of the other males. Incomplete molt that results in retention of old rectrices appears to be widespread, if infrequent, in bee hummingbirds (Pyle et al. 1997), and retention of juvenile rectrices into adulthood impaired dive-sound production in a Calliope Hummingbird (Selasphorus calliope) (Clark 2011).

No Chilean Woodstar rectrices were available for testing in the wind tunnel, but because of the match between the kinematics and the sound recordings, we hypothesize that R3, R4, and/or R5 produce the high-pitched tones of their dive sound with their wispy tips (Fig. 5). The shapes of the feather tips are similar to the wry outer rectrices of the White-bellied Woodstar (Chaetocercus mulsant), so perhaps the modes of flutter are also similar (Clark et al. 2011). The Chilean Woodstar’s high-pitched tones, the higher of which is above 10 kHz, represent the highest-pitched sonation currently known in the class Aves. The smallest or narrowest feathers are expected to vibrate at the highest frequencies (Clark et al. 2013), and, consistent with this, the outer tips of R3, R4, and R5 in this species are essentially reduced to filaments less than a millimeter wide (Fig. 7).

In the Peruvian Sheartail, our wind-tunnel data suggested that R3, R4, and R5 may all contribute to production of the dive sound, contra our hypothesis that R2 generated the sound. Multiple nonharmonic tones between 0.5 and 1.5 kHz are generated during this species’ displays (Fig. 1C), indicating multiple, independent sources of sound. Our wind-tunnel experiments suggested that all three of these feathers were capable of producing sounds within this frequency range. Whether one of these feathers is more important than the others at producing this sound is unclear and could be resolved by manipulative experiments on the tails of wild birds.

It is unclear whether the dive sound produced by the tail of Peruvian Sheartail has a communication function. The sound is quiet and not produced exclusively in a stereotyped, specific fashion, in the way that the tail-generated sounds of most of its relatives are produced. Other species produce pulses of sound with a spread of the tail (e.g., Feo and Clark 2010). The
behavior of these other species suggests that spreading the tail is a stereotyped behavior to create the sound. By contrast, in the Peruvian Sheartail, the tail is held stiffly split during nearly the entire display, including as the bird hovers and sings. The critical velocity of airflow needed for its rectrices to generate sound is low (Table 1), and males routinely exceed this speed during ordinary flight, explaining why we heard the dive sound in a variety of flight contexts.

The greatly elongated R2 of the Peruvian Sheartail appears to serve as a visual signal during courtship displays (Fig. 2F), as males spread the tail widely and hold it nearly continuously in this posture during shuttle displays. During display, all of the rectrices project laterally (Fig. 2F), so that the surface of the tail is essentially “split” in two. As a point of comparison, the outer rectrices of the Marvelous Spathuletail (Loddigesia mirabilis) also attain a distinctive orientation during display, which Zusi and Gill (2009) demonstrated is achieved through normal spreading of the tail to an extreme angle. To generate the unique posture of the Peruvian Sheartail’s inner rectrices, the entire rectricial bulb into which all of the rectrices attach must rotate as a unit, in order to allow the inner rectrices to project laterally. This posture appears to be a synapomorphy shared with the Purple-collared Woodstar (Myrtis fanny) and Short-tailed Woodstar (Myrmia micrura), as these taxa also “split” the tail during display in a nearly identical fashion (CJC, unpubl. data). The Purple-collared Woodstar also produces a syllable similar to syllable d (Fig. 1A, 3A), reinforcing the impression that these four taxa form a monophyletic unit.

The Chilean Woodstar’s vocal song resembles a wing trill, both in acoustic qualities (Fig. 5A) and in timing: it is often produced just after takeoff, recalling of the wing trill of a male Broad-tailed Hummingbird leaving his perch. Yet it is clearly a vocalization, as perched birds produce it, and the true wing trill produced during the shuttle display was less tonal (Fig. 5). The song’s trill rate is about 70 Hz, within the range of wingbeat frequencies attained during the shuttle display. The similarities between this vocalization and the wing trills of some relatives suggests it could be an independently evolved instance of a match between nonvocal and vocal sounds, similar to that observed in Calypte hummingbirds (Clark and Feo 2010) and in Pseudocolopteryx flycatchers (Bostwick and Zyskowski 2001).

**MATING SYSTEM AND TERRITORIALITY**

Our observations suggest that male Chilean Woodstars display in a lek. Males placed their courtship territories above dense thickets, a habitat that has become scarce in Azapa and Vítor with the spread of agriculture. Over several days of observations, one male received repeated visits from females (plus copulation), while we never saw a female on the territory of close neighbors, implying a high reproductive skew. Several males had no flowers (i.e., resources) in their territories, while a large nearby patch of blooming chañar was apparently undefended, suggesting that floral resources did not play a role in territory formation.

Male Chilean Woodstars engaged in interspecific competitive interactions with nearby territorial male Peruvian Sheartails, and we have no evidence of overlap of territories of males of these two species. This is consistent with the interspecific territoriality of other bee hummingbirds that breed sympatrically (e.g., Pitelka 1951). Pitelka (1951) documented that competition for courtship territories reduced the habitat’s carrying capacity for each competing species, which suggests that the Peruvian Sheartail may have similar effects on the Chilean Woodstar. In contrast, some territorial male Oasis Hummingbirds ignored intruding Peruvian Sheartails, resulting in overlap in the territories of males of these two species at some sites. Elsewhere Oasis Hummingbirds attacked and displaced territorial Peruvian Sheartails, so there is competition between these two species.

Male Peruvian Sheartails tended to have blooming *T. fulva* on their territories, but whether males held territories for their resource value was unclear. We rarely saw female Peruvian Sheartails near males’ territories, and females that we did see were contending with the aggressive advances of one or more males, so it is unclear whether females could sample or assess a male’s resources. Further insights into these mating systems, and by extension the potential effects of interspecific territoriality between the Peruvian Sheartail and Chilean Woodstar, could be assessed by comparing food available on courtship territories in Azapa to that in Vítor, as *T. fulva* is abundant in Azapa and absent from Vítor.

**HYBRID CHILEAN WOODSTAR × PERUVIAN SHEARTAIL**

Many hybrid combinations of hummingbirds are known (Banks and Johnson 1961, Graves 2007). The morphology of most hybrids is intermediate between that of the parental species (Graves 2008). The hybrid Peruvian Sheartail × Chilean Woodstar we studied represents a small exception to this pattern: both R1 and R4 were longer than in either parental species (Table 2, Fig. 7). In hummingbirds, the evolution of neighboring tail feathers is correlated, suggesting they are not independent characters (Clark 2010, unpubl. data). We hypothesize that R1 was longer in the hybrid because of pleiotropic effects from a small number of genes in the Peruvian Sheartail that code for an elongated R2; likewise that R4 was elongated because of a small number of genes from the Chilean Woodstar that code for an elongated R3 and/or R5. Hybrids may also exhibit transgressive courtship behaviors (Clark et al. 2012, Wells et al. 1978), but we detected no clear examples of that in this individual (Table 3). Several of the behaviors matched those of one parent closely, rather than showing intermediary, suggesting they may be under relatively simple genetic control (Table 3).
The hybrid’s song had two syllables (Fig. 8B), fewer than Peruvian Sheartail’s four, and more than Chilean Woodstar’s one. The scolding call was similar to syllables from the Peruvian Sheartail’s song, and the hybrid’s scolding call did not closely match its song. This was odd, as it is in contrast with both parents, each of which have scolding calls similar to their songs (Fig. 1A, C and 5A, B).

We attribute the lack of a tail-generated dive sound of the hybrid (Fig. 8C) to the small size of its dives (Fig. 9), which likely resulted in the hybrid failing to reach high speed at the bottom of the dive, and therefore it may not have exceeded the critical velocity for sound production by its tail feathers (Clark et al. 2011).

CONSERVATION IMPLICATIONS FOR THE CHILEAN WOODSTAR

Our diagnosis of a hybrid Chilean Woodstar × Peruvian Sheartail is evidence of interspecific competition for mates between the two species. Genetic data indicate that the hybrid’s mother was a Chilean Woodstar (van Dongen et al. 2013). Males of many bee hummingbirds display to and copulate with anything resembling a female of their species, including newly fledged chicks (TJF, pers obs.; Armstrong 1988, Stiles 1973), heterospecific females (whether wild, caged, or stuffed mounts), or inanimate objects roughly the size of a female (Fig. 6D). Therefore we expect that males of either species would display to and mate with females of the other species, given the opportunity.

The hybrid is attributable either to forced copulation or to female choice (Randler 2002). Despite the parental species’ morphological similarities, their courtship displays and songs are distinct, suggesting that females have ample opportunity for species recognition and discrimination. Male Peruvian Sheartails pursue females aggressively during courtship, and females perched deep in thick bushes in apparent defense (Fig. 2C). Male Peruvian Sheartails may harass and attempt to force-copulate with female Chilean Woodstar by using behavioral strategies that female Chilean Woodstar have not coevolved to deal with. On the other hand, Chilean Woodstars have shorter wings and higher wingbeat frequencies than Peruvian Sheartails (Table 2), characteristics correlated with maneuverable flight performance and success in agonistic interactions (Altshuler 2006), and this is likely the reason why male Chilean Woodstars tend to dominate Peruvian Sheartails in individual interactions (van Dongen et al. 2013). Therefore, on the basis of their flight morphology, female Chilean Woodstars should be better equipped to evade unwanted attention from male Peruvian Sheartails than are female Peruvian Sheartails.

Alternately, the mother may have voluntarily mated with a male Peruvian Sheartail. This could occur if she were unable to find a suitable male Chilean Woodstar, i.e., an Allee effect of the population of the Chilean Woodstar (Stephens et al. 1999) now being small and fragmented. In 2010 we only found two adult males holding courtship territories at the locality where we caught the hybrid. The hybrid was a product of a prior breeding season, and not necessarily from the locality where we found him, so we cannot make firm inferences regarding the availability of male Chilean Woodstars to his mother. Nevertheless, in Azapa the Peruvian Sheartail is now much more common than the Chilean Woodstar (Estades and Aguirre 2010, Estades et al. 2007).

We have no evidence of past introgression between the two species (van Dongen et al. 2013), suggesting that, so far, backcrosses have been too rare to detect. However, if the hybrid we discovered is related to the recent crash of Chilean Woodstar’s population in Azapa, additional hybrids and introgression should be expected in the future. The well-studied North American bee hummingbirds hybridize regularly, but it seems unlikely that hybrids are more common than one in several thousand individuals. By contrast, the Chilean Woodstar, with the few remaining local populations numbering in the dozens to hundreds (Estades and Aguirre 2010), even a single hybrid is a comparatively large fraction of the population and therefore is of conservation concern for the Chilean Woodstar (Allendorf et al. 2001).

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