



## THE DISPLAYS AND SONATIONS OF THE BLACK-CHINNED HUMMINGBIRD (TROCHILIDAE: *ARCHILOCHUS ALEXANDRI*)

TERESA J. FEO<sup>1,2,3</sup> AND CHRISTOPHER J. CLARK<sup>1,2</sup>

<sup>1</sup>Museum of Vertebrate Zoology, 3101 VLSB, University of California, Berkeley, California 94720, USA; and

<sup>2</sup>Present address: Department of Ecology and Evolutionary Biology, 21 Sachem Street, Yale University, New Haven, Connecticut 06511, USA

**ABSTRACT.**—Studies on the sonations (nonvocal communicative sounds) of birds have revealed a wide diversity of mechanisms and functions. We describe the kinematics and sounds of the display dive and shuttle display of the male Black-chinned Hummingbird (*Archilochus alexandri*). Males produced an integrated series of trilled and tonal sounds during their displays. Through a combination of experiments on wild birds, experiments on isolated feathers in the laboratory, and comparisons between high-speed video and audio recordings, we show that the display sounds are sonations produced by feathers. The timing of the trilled sounds during both the shuttle and dive displays corresponded to the wingbeat kinematics, which suggests that they are produced by the wings. These trills were qualitatively similar to the wing trills reported for other species of hummingbirds, but the mechanism of sound production remains unclear. The production of the tonal sounds during the display dive corresponded to tail spreads, and experiments show that this sound was produced by fluttering of the tip of the outer tail feather, rectrix 5 (R5). Hummingbirds in the genus *Calypte* also produce dive sounds with R5, but sound is instead generated by the trailing vane of the feather. *Calypte* and Black-chinned Hummingbirds differ in the shape of the tip of R5, and we hypothesize that this difference in shape affects which mode of flutter is activated by airflow. Received 12 December 2009, accepted 24 June 2010.

Key words: *Archilochus alexandri*, display, hummingbird, mechanical sound, sonation, tail feather, wing trill.

### Despliegues y Sonidos no Vocales de Comunicación en *Archilochus alexandri* (Trochilidae)

**RESUMEN.**—Los estudios sobre los sonidos no vocales producidos por las aves para comunicarse han revelado una amplia variedad de mecanismos y funciones. Describimos la cinemática y los sonidos asociados con dos tipos de despliegue en vuelo realizados por los machos del colibrí *Archilochus alexandri*. Los machos produjeron una serie integrada de sonidos trinados y tonales durante sus despliegues. Mediante una combinación de experimentos con aves silvestres, experimentos en plumas aisladas en el laboratorio y comparaciones entre vídeos de alta velocidad y grabaciones de audio, demostramos que los sonidos involucrados en el despliegue son producidos por las plumas. El momento en que los sonidos trinados fueron emitidos durante ambos tipos de despliegue correspondió con la cinemática del aleteo, lo que sugiere que estos sonidos son producidos por las alas. Esos trinos fueron cualitativamente similares a los trinos producidos por las alas que han sido documentados en otras especies de colibríes, pero el mecanismo de producción del sonido aún no ha sido aclarado. La producción de los sonidos tonales durante el despliegue de vuelo en picada correspondió con la apertura de las plumas de la cola y los experimentos mostraron que estos sonidos fueron producidos por el movimiento vibratorio de la punta de la rectriz 5 (R5), la pluma externa de la cola. Los colibríes del género *Calypte* también producen sonidos con la R5 al lanzarse en picada, pero lo hacen mediante el vexillo posterior de la pluma. Ya que *Calypte* y *A. alexandri* difieren en la forma de la punta de la R5, planteamos la hipótesis de que esta diferencia en forma afecta cuál modo de movimiento y producción de sonido es activado por el flujo de aire.

SONATIONS ARE NONVOCAL, or mechanical, sounds that are produced by animals and have a communicative function (Bostwick and Prum 2003). Examples include the wing sounds of hummingbirds (Family Trochilidae; Miller and Inouye 1983, Hunter 2008) and doves (Family Columbidae; Hingee and Magrath 2009), the knee-clicks of bull Eland Antelopes (*Tragelaphus oryx*; Bro-Jørgensen and Dabelsteen 2008), and the foot drumming of rodents

and rabbits (Orders Rodentia and Lagomorpha; Randall 2001). In birds, sonations are acoustic signals that are produced by any structure other than the syrinx, and they have been described for many species (Bostwick 2006). Sonations can be produced by a variety of structures, such as the bill, tail, wings, or feathers, and by a variety of mechanisms, such as percussion, stridulation, or resonant flutter (Bostwick and Prum 2003, 2005; Clark and Feo

<sup>3</sup>E-mail: [teresa.feo@yale.edu](mailto:teresa.feo@yale.edu)

2008). Investigations of nonvocal sounds will enhance our understanding of the evolution of alternative modes of acoustic signal production and avian communication.

Hummingbirds derive their common name from the “humming” sounds that their wings produce during flight. Flapping wings create changes in air pressure at a rate equal to the wingbeat frequency (WBF), and at sufficiently high frequencies, human ears perceive the pressure fluctuations as sound (audio speakers use a similar mechanism to produce sounds). Hummingbirds hum because they regularly flap their wings at frequencies that we can hear. This fundamental sound of beating wings is called the “wing hum” and has a pitch, or acoustic frequency, that is equal to the WBF (Hunter and Picman 2005).

Flapping wings can also produce additional sounds, termed “wing trills” (Hunter and Picman 2005). Examples of wing trills include the “whirring” sounds produced by flying male Broad-tailed Hummingbirds (*Selasphorus platycercus*) and Streamertails (*Trochilus polytmus*). The wing hum is an incidental sound present in all flying hummingbirds, whereas wing trills are additional acoustic signals produced only by some species, often only by the male, and there is evidence that they are used in communication (Miller and Inouye 1983, Hunter and Picman 2005). These sonations have been given a variety of names, which makes it important to clarify the terms “trill,” “wing trill,” and “trill rate.” A trill is any sound composed of a rapid series of notes, and the term does not imply a specific mechanism of sound production; either a clarinet or a Chipping Sparrow (*Spizella passerina*) can produce a trill with its reed or syrinx, respectively. Wing trills are a specific type of trilled sound produced by a mechanism that involves flapping wings. The trill rate is a measure of the frequency of note repetition for a trilled sound.

Wing trills are higher-pitched sounds than wing hums and appear to be produced by the primary feathers. Clark (2008) demonstrated that air rushing over the primary feathers of the male Streamertail induces the feather tips to flutter and produce sound with each downstroke. The proposed mechanism of sound

production is resonant flutter, in which air flow induces a feather to flutter at a resonant frequency that is set by the mass, geometry, and stiffness of the feather (Clark and Feo 2008). The trill rate of a wing trill can be either equal to or double the WBF, depending on whether the primaries produce sound once per wingbeat or twice, once with the downstroke and once with the upstroke. Generally, a wing trill has an acoustic frequency that is equal to the flutter frequency of the sound-producing feathers and a trill rate that matches (or is double) the WBF.

In addition to generating wing sounds, some hummingbirds also sonate with tail feathers. During the breeding season the pugnacious and flamboyant males of many species perform elaborate aerial display dives for females. Males produce stereotypic, species-specific sounds during these displays that are called “dive sounds.” Both male Anna’s Hummingbirds (*Calypte anna*) and male Costa’s Hummingbirds (*C. costae*) produce their dive sound with the outermost tail feathers (Clark and Feo 2008, 2010). In both species, the high speeds reached during the dive cause the trailing vane of rectrix 5 (R5) to flutter and produce sound when the tail is spread.

*Archilochus* and *Calypte* are closely related genera (McGuire et al. 2007), and male Black-chinned Hummingbirds (*Archilochus alexandri*) also perform aerial displays that are likely homologous with the displays of *Calypte*. Male Black-chinned Hummingbirds perform two distinct types of displays, shuttle displays and display dives, and each is accompanied by the production of stereotypic sounds (Fig. 1). When performing a shuttle display, males approach within a few centimeters of a female with gorget flared and rapidly fly side-to-side (laterally) along a horizontal line ~0.5 m wide while producing pulses of trilled sound (Baltosser and Russell 2000; Fig. 1A, C). When performing display dives, males ascend to heights of 10–15 m and repeatedly dive back and forth (as if tracing out the swing of a pendulum) in broad U-shaped arcs 15–20 m wide while producing a series of trills and tones (Pytte and Ficken 1994; Fig. 1A, B).

Pytte and Ficken (1994) described the two main elements of the dive sound, a broad-frequency trilled “element X” and a series

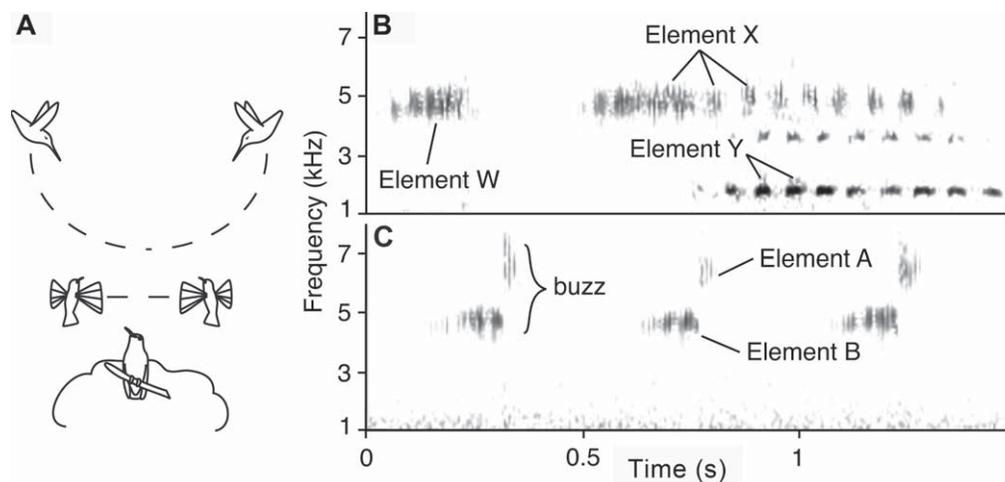


FIG. 1. The displays of male Black-chinned Hummingbirds. (A) General movements of the display dive (above) and shuttle display (below) in relation to a perched female (not to scale; dives are 10–15 m high and 15–20 m wide, whereas shuttles are 0.5 m wide). (B) Dive sound with elements W, X, and Y labeled. (C) Shuttle display sound showing three buzz units; elements A and B are labeled.

of tones collectively referred to as “element Y” (Fig. 1B). They argued that both elements of the dive sound were vocal because the frequency and temporal patterns of the dive sounds were similar to other known Black-chinned Hummingbird vocalizations. However, our work with Anna’s and Costa’s hummingbirds has falsified the hypothesis that an acoustic similarity between two sounds implies a similar mechanism. Experiments have indicated that the dive sounds in these two species are sonations produced by tail feathers, even though the dive sound of each species is acoustically similar to its song (Clark and Feo 2008, 2010).

The purpose of the present study was to further explore the use of sonations in the displays of birds, and specifically to determine the source of Black-chinned Hummingbird display sounds. Through comparisons of high-speed video with audio recordings of the displays, manipulations on the tail feathers of wild males, and laboratory tests of the ability of tail feathers to produce tonal sounds, we show that the tips of R5 produce the tones of the dive sound and that the wings produce the trills of both the dive and shuttle displays.

#### METHODS

**Field experiment.**—All field work on wild Black-chinned Hummingbirds was conducted at the California Audubon Society’s Kern River Preserve, Weldon, Kern County, California (35.6688°N, 118.3034°W) in June of 2007 and 2008. Individual wild males were located on breeding territories by their consistent use of a few specific perches. Males generally held territories in open areas along the edges of meadows in cottonwood–willow riparian habitat. We elicited display dives from a male either by releasing a recently captured female or by placing a female in a cage on the male’s territory. The use of a stuffed mount of a female Anna’s Hummingbird was unsuccessful in eliciting dives from males.

Audio recordings of the display dives and shuttle displays were recorded in both years using a Sennheiser ME 67 shotgun microphone, sampled at 48 kHz using a 16-bit digital recorder (Marantz PMD 670), and saved as uncompressed WAV files. All audio recordings were analyzed using RAVEN, version 1.2.1 (Cornell Lab of Ornithology, Ithaca, New York). Spectrograms were created using a Hann function with a 512 sample window and 50% overlap. High-speed videos of the display dives were recorded in 2008 using a Phantom HD camera (Vision Research, Wayne, New Jersey; 500 fps, 2,048 × 1,080 pixels) or an X-PRI F1 camera (AOS Technologies, Baden, Switzerland; 500 fps, 800 × 600 pixels). High-speed video was obtained opportunistically, and the cameras panned and zoomed to follow the bird. It was not possible to synchronize high-speed video of the flying birds with the corresponding audio recordings.

After we recorded display dives, males were captured with feeder traps that we placed on their territories. Each captured male was banded and marked with Liquid Paper for reidentification, given one of three tail manipulations, and then released back onto his territory. Black-chinned Hummingbirds have five pairs of tail feathers, and the outermost have a tapered tip (Fig. 2A, B). The tail manipulations were as follows: (1) pluck both R4, (2) pluck both R5, or (3) cut the tip off of both R5 at the start of taper (Fig. 2C). Three males were also placed in a cage to measure hovering WBF using high-speed video. It took males less than 2 days to resume

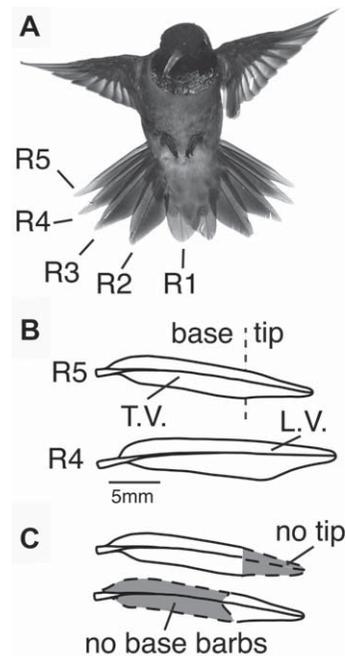


FIG. 2. Feathers of a male Black-chinned Hummingbird. (A) Male with rectrices 1–5 labeled (R1–R5) (photograph courtesy of Anand Varma). (B) Scaled line drawings of R5 and R4; the dotted line indicates the start of taper, L.V. = leading vane, and T.V. = trailing vane. (C) Drawing of a manipulated R5 with no tip (above) and no base barbs (below). Dashed line and shading delineate the part of the feather that has been removed.

active defense of their territories after they were released. Once a male had resumed territorial behavior, we elicited postmanipulation dives within 2 weeks of manipulation. Plucked tail feathers regrow in ~5 weeks (C. J. Clark pers. obs.).

**Audio and video measurements.**—The display sounds of a wild male (Fig. 1) included both trilled sounds with a relatively broad acoustic frequency (dive elements W and X and shuttle elements A and B) and pure bell-like tones with a distinct fundamental acoustic frequency (dive element Y). We measured eight variables for each dive sound and five variables for each shuttle sound (summarized in Fig. 3). We use the term “note” to refer to an individual unit of sound and “syllables” to refer to groups of notes. Acoustic frequencies were measured from the middle of the frequency range unless otherwise indicated.

Males alternated among three flight modes during the display dive: flapping, bounding, and gliding. The WBF was measured by counting the number of full strokes (upstroke to upstroke) per unit time. During a bound the bird tucked its wings in alongside its body, and during a glide the wings were held stationary, away from the body. Males also alternated between spreading and shutting the tail. The length of time the tail was spread was measured from when the tail was halfway spread through to halfway shut, and the length of time the tail was shut was measured from when the tail was halfway shut through to halfway spread.

For each high-speed video of a display dive, we measured the following variables: the WBF when the bird was turning around at the top of the dive, the length of the bound in seconds, the WBF at

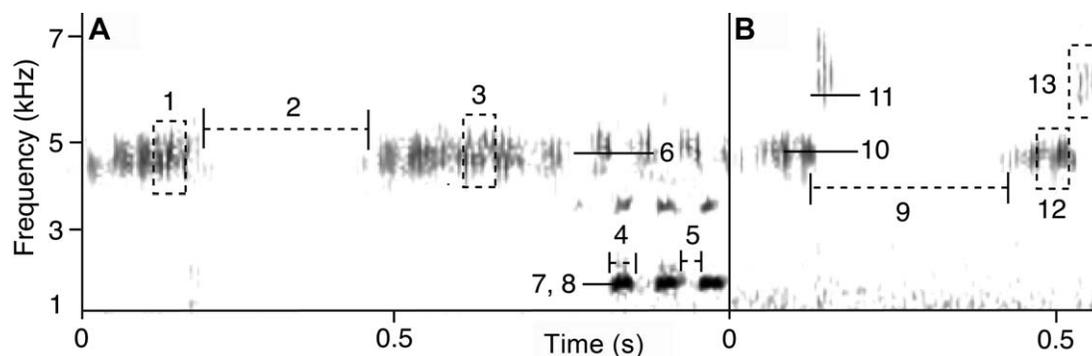


FIG. 3. Spectrograms showing measured parameters of (A) the display dive and (B) the shuttle display of male Black-chinned Hummingbirds. 1 = element W trill rate, 2 = gap of silence between element W and element X, 3 = element X trill rate, 4 = average duration of three-element Y notes, 5 = average interval of silence between three-element Y, 6 = element X acoustic frequency, 7 = minimum acoustic frequency of element Y, 8 = maximum acoustic frequency of element Y, 9 = duration of one shuttle buzz cycle, 10 = element A acoustic frequency, 11 = element B acoustic frequency measured from the bottom of the frequency range, 12 = element A trill rate, and 13 = element B trill rate.

the bottom of the dive while the male was spreading and shutting its tail, the length of each time the tail was spread, and the length of each time the tail was shut.

*Laboratory experiments.*—The tail feathers that were used in the lab experiments were collected from wild males during the field work. We placed individual feathers in front of a jet of air or wind tunnel to test their ability to produce sounds that matched the tonal element Y of the dive. We did not have permission to collect primary feathers and therefore did not test their ability to produce the wing sounds.

The experimental setup that we used to test the feathers is described more fully in Clark and Feo (2008). We utilized two complementary protocols to identify the mechanism responsible for sound production. First, we placed the feathers in a jet of air (at speeds nominally exceeding  $30 \text{ m s}^{-1}$ ) and manipulated their orientation until they began to produce sounds. We filmed feathers with a Fastcam APX RS (Photron, San Diego, California; 20,000 or 30,000 fps) and simultaneously recorded sounds with the same audio setup as was used in the field work. The purpose of this was to identify which part of the feather fluttered as sounds were produced. However, the airflow of the jet was of poor quality and too small to contain the entire feather in the airflow.

To complement data from the jet, we also placed the feathers in a wind tunnel with better airflow than the jet. The feathers were mounted perpendicular to airflow and rotated through a range of angles of attack to ensure that orientation did not affect a feather's ability to produce sound. Sounds produced by the feathers in the tunnel were recorded with an ME-67 microphone (Sennheiser, Old Lyme, Connecticut) placed upwind from the feather. Feathers were filmed with a monochrome Phantom Miro 4 high-speed camera (Vision Research; 20,000 fps) to test whether they exhibited the same mode of flutter that we measured in the jet of air.

After we recorded unmanipulated R5 feathers, we performed one of two manipulations to determine whether only a part of the feather was necessary to produce a particular sound: (1) we cut off the tip of the feather at the start of the taper or (2) we cut off all barbs below the start of the taper, leaving the shaft of the feather and the tip barbs intact (Fig. 2C). The feathers were then rerecorded postmanipulation in the jet or wind tunnel.

Averages are presented  $\pm 1$  SD. Recordings from the field have been deposited at the Museum of Vertebrate Zoology, University of California, Berkeley (accession no. 14571).

## RESULTS

*General observations on the displays.*—When a male noticed a female on his territory he would pursue her, and if she landed, he would then begin performing displays. Males would perform display dives, shuttle displays, or a combination of the two. Almost all of the shuttle displays that we observed were performed before or in between a bout of dives. Males would generally perform a bout of 5 to 15 dives and then perch for a short period. If the female remained on the territory, the male would then launch into another bout of dives and shuttles. Male Black-chinned Hummingbirds did not orient the dive toward the sun as Anna's Hummingbirds do (Hamilton 1965).

The average bout of dives was 7.5 dives performed in 18.5 s, and the longest bout was 17 dives in 40 s (27 bouts by 9 males). The average length of a shuttle display was 13.9 s and the longest was 45 s (26 shuttles by 8 males). One male performed a combination of shuttle displays and display dives continuously for 53 s. Males often panted when perched between bouts of dives, and the number of dives would often dwindle in successive dive bouts, sometimes down to only one or two dives before a male would take another break. These behaviors gave the impression that performing the display dives was physically demanding.

*The display dive sound.*—The dive sound of wild males (Fig. 1B) was composed of a series of broad-frequency trilled syllables and low-pitched tonal notes. The dive sound started with one or two syllables of element W, followed by a relatively long gap of silence, followed by the alternating production of elements X and Y (Fig. 1B). Element W was produced as the male turned around at the top of a dive and began his descent, and elements X and Y were produced at the bottom of the dive as the male was passing over the female. Element Y tones included both the fundamental acoustic frequency and the second harmonic.

We recorded the dive sounds of 9 wild males. For each dive sound, we measured eight variables (Fig. 3A), which are

TABLE 1. Measures of the dive sounds and kinematics of male Black-chinned Hummingbirds (WBF = wingbeat frequency; for description of elements W, X, and Y, see text and Fig. 1; for kinematics, see Fig. 5).

Sound	Mean $\pm$ SD	$n^a$	Kinematics	Mean $\pm$ SD	$n^a$
1. W trill rate (Hz)	84.4 $\pm$ 4.44	14 (4)	I. Turning WBF (Hz)	81.8	1 (1)
2. Gap length (s)	0.208 $\pm$ 0.063	18 (4)	II. Bound length (s)	Present <sup>b</sup>	—
3. X trill rate (Hz)	82.0 $\pm$ 4.49	49 (9)	III. Bottom WBF (Hz)	78.5 $\pm$ 3.09	2 (2)
4. Y note (s)	0.045 $\pm$ 0.005	42 (8)	III. Tail spread (s)	0.048 $\pm$ 0.007	2 (2)
5. Time between Y notes (s)	0.031 $\pm$ 0.003	42 (8)	III. Tail shut (s)	0.026 $\pm$ 0.005	2 (2)
6. X frequency (kHz)	4.71 $\pm$ 0.164	49 (9)			
7. Minimum Y frequency (kHz)	1.66	53 (9)			
8. Maximum Y frequency (kHz)	2.26	53 (9)			

<sup>a</sup> $n$  = number of dives (number of males).

<sup>b</sup>A single video captured only a portion of a bound; therefore, no value is presented.

summarized in Table 1. Element W was heard by ear during most display dives, but our sample sizes for measures of element W and the following gap of silence were low because the sound was too faint to analyze in the spectrograms of most dives. This was apparently because males were farther away from the microphone when they produced element W than when they produced sounds at the bottom of the dive. Successive notes of element Y either slightly increased or decreased in acoustic frequency. We measured the minimum and maximum acoustic frequency of element Y in each dive and present the combined frequency range for all dives.

*Effects of the field manipulations on the dive sound.*—Of the 6 males that we manipulated, 2 had R4 removed, 3 had the entire R5 removed, and 1 had just the tips of R5 removed. All 6 birds continued to produce the trilled elements W and X after manipulation. The 2 males with no R4 produced element Y in an average of 99% (27 of 27 and 74 of 75) of the dives before manipulation, and they continued to produce element Y after manipulation in an average of 97% (11 of 11 and 159 of 167) of their dives (Fig. 4A).

On the other hand, males with manipulated R5 never produced element Y (Fig. 4B). The 3 males with no R5 produced element Y in 100% ( $n = 9, 5, 14$  for a total of 28) of the dives before manipulation and in 0% ( $n = 16, 10, 3$  for a total of 29) of dives after manipulation. Similarly, 1 male with the tip of R5 removed produced element Y in 96% (24 of 25) of dives before manipulation but

in 0 of 11 dives after manipulation. In aggregate, our experimental manipulations suggest that males need the tips of R5 to produce element Y of the dive sound, whereas R4 is unnecessary.

We compared the dive sounds of 1 male before and after removing R4 and found only one variable that differed significantly. We measured 6 dives premanipulation and 6 dives postmanipulation, with the exception that postmanipulation measures of element W trill rate and gap length were from only 4 dives. The interval between each element Y note increased from an average of 0.029  $\pm$  0.003 s to an average of 0.034  $\pm$  0.003 s after removing R4 (unpaired  $t$ -test,  $P = 0.01$ ). This represents a change in the timing between element Y notes, although neither the acoustic frequency nor the length of the notes themselves changed. The other seven measured variables did not differ significantly after manipulation (unpaired  $t$ -test,  $P > 0.1$ ).

*Display dive kinematics.*—High-speed video was obtained opportunistically because it was difficult to predict the location and trajectory of a dive until a male began to display. We recorded high-speed video of 2 unmanipulated males each performing 1 dive, and 21 dives from 1 manipulated male (R4 removed) as it performed >100 dives in the course of an afternoon. Each high-speed video showed only a portion of a dive, ending when the bird flew out of frame or behind a plant. Therefore, sample sizes for specific kinematic stages vary. Because the kinematics appeared to be highly stereotyped and there was no obvious difference in the sequence of movements among the 3 males (either unmanipulated or manipulated), videos from all 3 males were used to reconstruct the entire kinematic sequence. The kinematic measures of the 2 unmanipulated males are presented in Table 1, and those of the manipulated male in Table 2.

The display dive consisted of five stages: (I) turning around, (II) bounding, (III) tail spreading, (IV) gliding, and (V) ascending (Fig. 5). In stage I, males began a dive by ascending to a height of 10–15 m and then turned around with 1 or 2 bouts of rapid flapping (Fig. 5A). During the descent in stage II, males tucked their wings along their body and bounded (Fig. 5A). In stage III, males first resumed flapping at the bottom of the dive and then began to repeatedly spread and shut the tail (Fig. 5B). As males began to rise out of a dive in stage IV, they held their wings out and glided as they spread their tail one or two more times. Males completed their ascent out of the dive in stage V with combinations of gliding, bounding, and flapping.

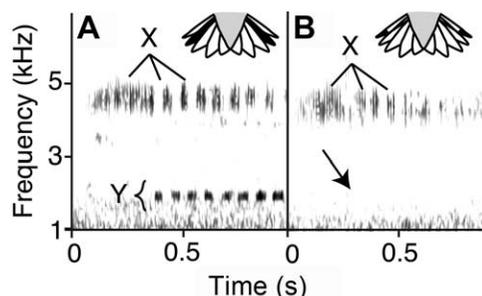


FIG. 4. Dive sounds of manipulated male Black-chinned Hummingbirds (element W present in both but not shown); drawings show the full tail with the removed feathers or parts in black. (A) No R4; both element X and element Y are present. (B) No tips of R5; element X is present but element Y is missing (arrow).

TABLE 2. Comparison of the rate or duration of display-dive kinematics with the rate or duration of the dive-sound elements of one manipulated male with no R4 (WBF = wingbeat frequency; for description of elements W, X, and Y, see text and Fig. 1; for kinematics, see Fig. 5).

Kinematics	Mean $\pm$ SD	$n^a$	Sound	Mean $\pm$ SD	$n^a$	$P^b$
I. Turning WBF (Hz)	81.7 $\pm$ 7.04	9	1. W trill rate (Hz)	84.2 $\pm$ 1.81	4	0.5
II. Bound length (s)	0.099 $\pm$ 0.042	12	2. Gap length (s)	0.237 $\pm$ 0.032	4	<b>&lt;0.01</b>
III. Bottom WBF (Hz)	79.8 $\pm$ 2.95	21	3. X trill rate (Hz)	80.5 $\pm$ 3.23	6	0.7
III. Tail spread (s)	0.046 $\pm$ 0.017	6	4. Y note (s)	0.043 $\pm$ 0.04	6	0.7
III. Tail shut (s)	0.033 $\pm$ 0.006	3	5. Time between Y notes (s)	0.034 $\pm$ 0.003	6	0.7

<sup>a</sup> $n$  = number of dives.

<sup>b</sup>Unpaired  $t$ -test; significant  $P$  values are in bold.

The WBF values observed during the dives were relatively high. The average hovering WBF was 54.1  $\pm$  7.2 Hz ( $n$  = 3 males). In general, the WBFs observed during the display dives were dramatically higher than the WBFs of males hovering in a cage (Table 1). The highest recorded WBF, 93.4 Hz, was from the male with manipulated R4 during stage I of a dive. This represents a 98% increase in WBF compared to the same male's hovering WBF of 47.3 Hz.

In some videos, the wing stroke amplitude appeared to decrease each time the tail was spread at the bottom of the dive as compared to when it was shut. Because of uncertain camera angles this decrease could not be quantified. There was no significant difference between the WBF when the tail was spread or shut during the bottom of the dive (paired  $t$ -test;  $P$  = 0.4,  $n$  = 8 dives). This suggests that the males decreased the amplitude of the wing stroke, but not the WBF, when they spread their tails.

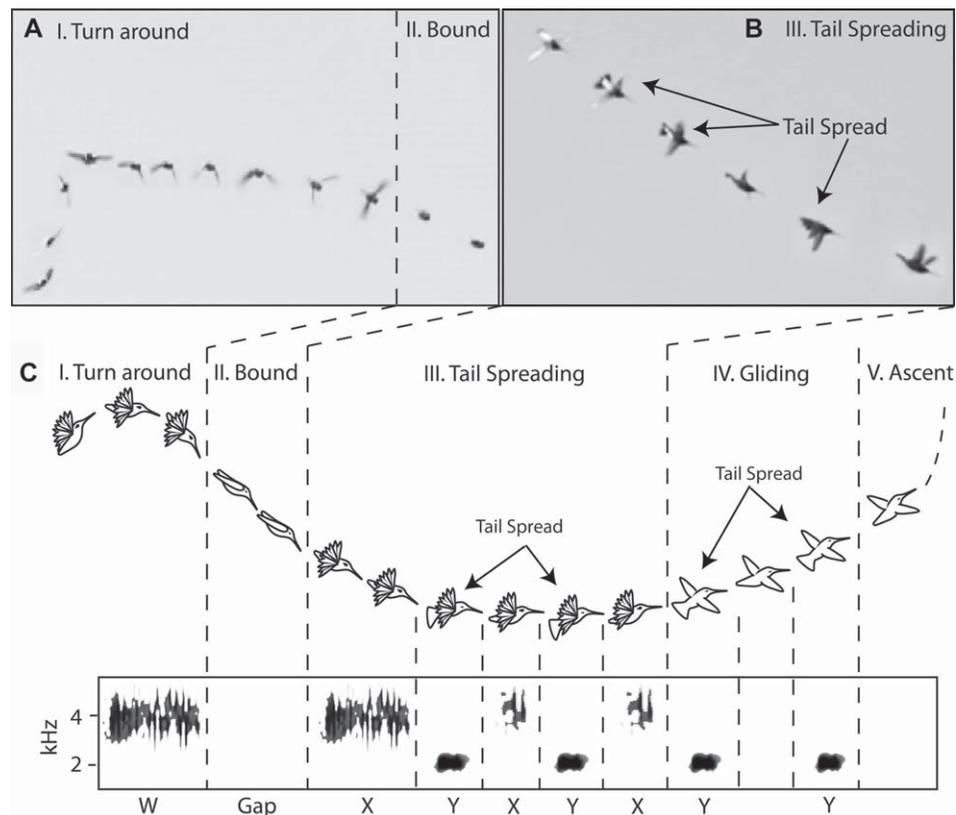


FIG. 5. Kinematics of the display dive of male Black-chinned Hummingbirds. (A) Composite image from high-speed video showing stages I and II; the male is flapping while he turns around and then begins his descent with a bound (wings tucked by sides). (B) Composite image of stage III; the male begins spreading and shutting its tail in alternating pulses while continuously flapping. Frames have been dropped for clarity, and the timing between frames in the composites varies. (C) The five stages of the display dive and a stylized spectrographic image of the dive sounds illustrating the match between kinematics and sound. The different stages are listed along the top, and the sound elements are listed along the bottom. Elements W and X are produced when the wings are flapping, and element Y is produced when the tail is spread.

*Comparison of the display dive and dive sound.*—We found a striking 1-to-1 relationship between the kinematics and sounds of the display dive (Table 2 and Fig. 5C). Video and audio of a manipulated male with R4 removed was used for the comparison because it was the only male with a sample size  $\geq 3$  for each of the kinematic measures. The manipulation did not affect this male's ability to produce any of the sounds we studied, because it continued to produce all three elements of the dive sound and there did not appear to be any major kinematic differences between its dives and those of the two unmanipulated males. As such, we believe that the relationship between flight postures and sound production can be generalized for unmanipulated males as well.

Both trilled elements W and X were produced during stages of the dive in which the male flapped his wings, whereas the gap of silence between the two trills occurred while the bird was bounding. We found no significant differences between the WBF at the top of the dive and the trill rate of element W, or between the WBF at the bottom of the dive and the trill rate of element X (Table 2). Also, the acoustic frequency of both elements fell within the 4- to 5-kHz acoustic frequency range for male Black-chinned Hummingbird wing trills reported by Hunter and Picman (2005). The close correlation between the trill rate and the WBF, and the match in acoustic frequency, suggest that both element W and element X are wing trills. On the other hand, the gap of silence between the two wing trills was significantly longer than the length of time that the bird spent bounding (Table 2). This suggests that the bound alone is not sufficient to explain the long gap of silence between the wing trills of the dive sound and that there must be some period in which the wings are flapping but not producing trills.

The series of tonal element Y notes were produced at the bottom of the dive during the same time that the male was repeatedly spreading and shutting his tail. We found no significant differences between the length of time the tail was spread and the length of the Y notes or between the length of time the tail was shut and the interval of silence between Y notes (Table 2). The close correlation between spread length and note length suggests that a note

of element Y is produced with each spread of the tail at the bottom of the display dive.

*The shuttle display.*—We recorded shuttle display sounds from 8 wild males, and for 10 shuttle sounds we measured each of the five variables (Fig. 3B). During a shuttle display males approached a female to within  $\sim 10$  cm and, while facing her, flew rapidly side-to-side, tracing out a horizontal arc (Fig. 1A). Males traveled laterally up to half a meter along this horizontal line. The shuttle sound was composed of a "buzz" sound that was continuously repeated for the duration of the display at an average rate of  $0.534 \pm 0.111$  Hz (Fig. 1C). A shuttle buzz was produced each time a male reached the end of his linear flight and reversed direction. No high-speed videos of males performing shuttle displays were obtained because males inevitably followed females into an obscuring bush or a tree before displaying.

Each shuttle buzz was composed of a long trilled element A syllable, immediately followed by a brief trilled element B syllable (Fig. 1C). Element A had an average acoustic frequency of  $4.60 \pm 0.011$  kHz, which is similar to the trilled elements of the dive sound. Element B was a higher- and broader-frequency trill than element A or the dive trills. The minimum acoustic frequency of element B was  $5.23 \pm 0.215$  kHz and was always higher than the acoustic frequency range of the corresponding element A.

The trill rate of element A was  $87.3 \pm 2.34$  Hz, and that of element B was  $89.4 \pm 3.36$  Hz. We compared the trill rate of elements A and B of the shuttle sound with the trill rate of element W of the dive sound and found no significant difference (*t*-test; element A,  $P = 0.2$ ; element B,  $P = 0.07$ ). The similar trill rates suggest that the shuttle sounds could also be wing trills like the dive elements, although it is not clear why element B has a higher acoustic frequency than any of the other wing trills.

*Laboratory experiments on isolated tail feathers.*—In general, rectrices produced sounds when the leading vane faced into the airflow and the shaft of the feather was perpendicular to the airflow (Fig. 6). We observed no dramatic differences in how the feathers behaved in the jet or in the wind tunnel; therefore, the results from

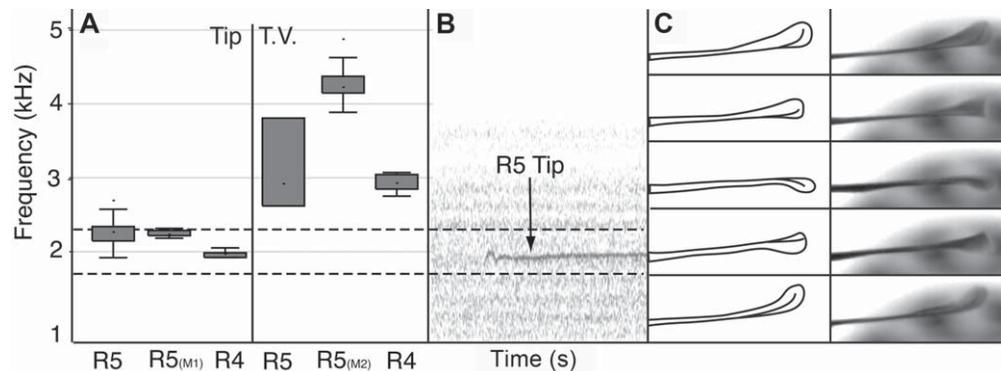


FIG. 6. The sounds produced in a jet of air by individual R5 and R4 tail feathers from male Black-chinned Hummingbirds. (A) The average frequencies of sound produced by isolated feathers with either the tip or the trailing vane (T.V.); m1 = manipulated feather with barbs below the tip removed (Fig. 2C), and m2 = manipulated feather with tip removed (Fig. 2C). (B) Spectrogram of the sound produced when the tip of an R5 flutters in a wind tunnel. The dashed lines in parts A and B indicate the minimum and maximum frequencies of dive element Y from 9 wild males. (C) High-speed video of the tip of the R5 fluttering up and down in a jet of air and producing a 2-kHz sound (right); line drawing of the feather in each frame for clarity (left). Frames are 6 ms apart. The feather is viewed edge-on, with the trailing vane closest to the viewer; the light gray object in the background of the video is the jet, and the direction of airflow is out of the frame toward the viewer.

both setups are combined below. The acoustic frequency of all sounds measured was highly correlated to the frequency of flutter from either the tip or trailing vane of the feather (regression,  $r^2 > 0.6$ , slope  $\approx 1.0$ ,  $P < 0.01$ ).

The tip of a male R5 produced sustained tonal sounds with fundamental frequencies that ranged from a minimum of 1.9 kHz to a maximum of 2.7 kHz with harmonics ( $n = 12$  feathers from 8 males; Fig. 6A, B), and the tip of male R4 feathers produced a tonal sound with a fundamental frequency ranging from 1.9 to 2.1 kHz with harmonics ( $n = 3$  feathers from 3 males; Fig. 6A). High-speed video of R5 and R4 in a jet of air revealed that the tip of the feather fluttered up and down at the same frequency as the fundamental acoustic frequency of the sound (Fig. 6C). The tips of male R5 and R4 feathers produced a range of frequencies that overlapped with the frequency range of dive element Y (Fig. 6). Although R4 is capable of producing sounds that match element Y, our field experiments suggest that only R5 is necessary for the males to produce sound (Fig. 4).

R5 with just the tip intact, base barbs removed (Fig. 2C), produced sound with a fundamental frequency ranging from 2.1 to 2.3 kHz ( $n = 3$  feathers from 2 males; Fig. 6A), and the average sounds produced by the manipulated R5 were not significantly different from the average sounds produced before manipulation (paired  $t$ -test: unmanipulated,  $2.20 \pm 0.129$  kHz; manipulated,  $2.26 \pm 0.040$  kHz;  $P = 0.5$ ). On the other hand, a manipulated R5 with no tip, only base barbs intact, produced sounds with a fundamental frequency ranging from 2.6 to 3.8 kHz, which did not match element Y ( $n = 1$  feather; Fig. 6A). These results suggest that only the tip of an R5 is needed to produce sounds that match element Y of the dive sound.

Male R5 and R4 feathers were also capable of producing a second tonal sound associated with fluttering of the trailing vane of the feather. R5 produced a trailing-vane sound with fundamental frequency ranging from 3.3 to 4.9 kHz with harmonics ( $n = 4$  feathers from 4 males; Fig. 6A), and R4 produced a trailing-vane sound with fundamental frequency ranging from 2.8 to 3.1 kHz with harmonics ( $n = 3$  feathers from 3 males; Fig. 6A). High-speed video of the R5 and R4 feathers revealed that the trailing-vane flutter was similar to the mode of flutter described for the R5 of both the Anna's and Costa's hummingbirds (Clark and Feo 2008, 2010). The frequency ranges for the trailing vane of the Black-chinned Hummingbird's R5 and R4 were much higher than the frequency range of element Y (Fig. 6A). Although this mechanism of sound production is physically possible, it appears that males did not make sounds with the trailing vane of the tail feathers in the wild.

## DISCUSSION

The dive display of the male Black-chinned Hummingbird is a stunning acrobatic feat that combines elevated wingbeat frequencies and coordinated movement of the wings and tail to produce a diversity of stereotyped sounds. Comparisons of the sounds and kinematics of the display dive revealed that the two are closely linked (Fig. 5C). Each sound, or lack thereof, corresponded to a particular movement—the trilled elements W and X were produced when the wings were flapping, and the tonal element Y notes were produced with each spread of the tail.

The match between wingbeat frequencies during the dive and the trill rates of the sounds suggests that elements W and X are wing

trills (trills produced by flapping wings). The feather manipulations on wild birds, timing of the tail spreads during the dive, and laboratory experiments indicate that the tonal dive element Y is produced by resonant flutter of the tip of R5. Additionally, the trilled elements A and B of the shuttle display are similar to the dive trills, which suggests that the shuttle display sounds are also wing trills.

Our results show that the dive sounds of the male Black-chinned Hummingbird are sonations produced by the wings and the tail and are not vocal as previously suggested (Pytte and Ficken 1994). The dive sound is composed of a combination of trills and tones in a stereotypic and complicated temporal pattern produced by two independently controlled structures. Male Black-chinned Hummingbirds demonstrate that sonations can rival vocalizations in complexity. This is a clear example of a bird using two different nonvocal, sound-producing structures in concert to produce an integrated sound.

*Wing trills.*—The wing trills described for the Black-chinned Hummingbird here and in other studies reveal a potential range of acoustic frequencies from 2 to 5 kHz. The frequencies presented here (4–5 kHz) match the frequencies described by Hunter and Picman (2005), and both are twice as high as the wing trills (2–3 kHz) described by Pytte and Ficken (1994). The outer primary feathers are responsible for producing the wing trills in other species of hummingbirds (Miller and Inouye 1983, Clark 2008). The shape of primary 10 is wider in the male Black-chinned Hummingbird than in the female Black-chinned Hummingbird or its sister species the Ruby-throated Hummingbird (*A. colubris*; Baltosser 1987), both of which produce acoustically different wing sounds (Hunter and Picman 2005). This suggests that primary 10 may play an important role in producing the wing trills. Further study can determine how the wing trills are produced and how the observed range of frequencies is created, especially the high acoustic frequency of element B in the shuttle display (Fig. 1C).

The wing trills of a male Black-chinned Hummingbird are silenced during three parts of the display dive. The first is the gap of silence between elements W and X, the second is the repeated interruption of element X to create the series of trill syllables at the bottom of the dive, and the third is the end of element X. The gap of silence between elements W and X and the end of element X are due to the cessation of flapping when the bird switches to a bound or a glide. However, the repeated interruption of element X at the bottom of the dive occurs while the male is continuously flapping its wings, without significant changes to the WBF.

The apparent mechanism causing the disruption in sound at the bottom of the dive is a decrease in wing-stroke amplitude while the tail is being spread. This decrease in stroke amplitude would reduce the mean wingtip velocity, because wingtip velocity is approximately proportional to the product of WBF and wing-stroke amplitude. Clark and Feo (2008) hypothesized that sounds produced by resonant flutter are only produced above a critical velocity of airflow. If a bird decreased its stroke amplitude while keeping WBF constant, the wingtip velocity would decrease and could fall below the critical velocity needed for sound production. As such, the modulation of stroke amplitude may serve to turn the production of a wing trill on or off while allowing the bird to continue flapping its wings at a high frequency.

Other species with pronounced wing trills fly silently at times, and modulation of both wing-stroke amplitude and the WBF are

likely methods of modulating the production of wing trills. Hunter and Picman (2005) showed that in the Black-chinned Hummingbird the trill is usually produced over a short portion of the wingbeat (apparently during the start of the downstroke). It is possible that other behavioral mechanisms to modulate trill production could include changing subtle aspects of wing kinematics during this portion of the wing beat, such as by altering aspects of wing rotation or modulating the exact shape of the wing (i.e., the orientation of the flight feathers in relation to each other).

*Changes in wingbeat frequency.*—The highest recorded WBF for a male Black-chinned Hummingbird was 93 Hz during a display dive, which exceeds the previous hummingbird record of 80 Hz reported for the Amethyst Woodstar (*Calliphlox amethystina*; Greenwalt 1960). The near doubling of WBF during a display is far greater than that observed in other hummingbird flight contexts. For example, Chai and Millard (1997) found that when male Black-chinned Hummingbirds lifted loads, their WBF increased from 51 Hz to only 60 Hz. Additionally, a contraction velocity of 93 Hz is relatively high, given that the flight muscles account for ~30% of the bird's body mass (Hartman 1961). Vertebrate striated muscle has performance limits—such as tradeoffs among muscle size, force production, and contraction velocity (Rome et al. 1996). For their size and contraction velocity, the flight muscles may be approaching intrinsic performance limits for flight during the display.

Increasing the WBF may serve to increase maneuverability during a display (Hedrick et al. 2009) or to sufficiently elevate the wingtip velocity to produce the wing trill. Comparable feats are achieved during the courtship sonations of the Flappet Lark (*Mirafra rufocinnamomea*; Payne 1973, Bertram 1977, Norberg 1991) and of *Manacus* spp. (Bostwick and Prum 2003), in which males double their WBF while creating percussive sounds.

*Mechanical sounds and feather shape.*—Black-chinned, Anna's, and Costa's hummingbirds all use the R5 to produce at least a portion of their dive sounds (Clark and Feo 2008, 2010). However, the Black-chinned Hummingbird uses a different mode of feather flutter. The Anna's and Costa's hummingbirds both use the trailing vane, whereas the Black-chinned Hummingbird uses the tip. The most obvious difference in the R5 is the shape of the tip: Anna's and Costa's Hummingbirds have a rounded tip whereas the Black-chinned Hummingbird has a tapered tip. The shape of the feather may play a role in determining how the feather produces sound.

We propose two hypotheses for how the shape of the feather might influence the mode of flutter. First, the shape of the feather may affect which mode of vibration is most easily excited by airflow. During tests of feathers in the laboratory it seemed that the R5 of Black-chinned Hummingbirds readily made the tip sound, but we had to spend much more time orienting the feather before it would produce a trailing-vane sound. On the other hand, the feathers of Anna's and Costa's hummingbirds readily made a trailing-vane sound (Clark and Feo 2008, 2010). These qualitative observations gave the impression that the feathers of *Calypte* spp. were more prone to flutter along the trailing vane than those of the Black-chinned Hummingbird.

A second way in which the shape might influence the mode of feather flutter is by creating gaps or spaces between feathers so that they are free to vibrate in a particular mode. Male Broad-tailed Hummingbirds make a persistent wing trill during flight, and experiments on wild birds have shown that a gap created by the

strongly emarginated primary 10 is at least partly responsible for the sound (Miller and Inouye 1983: fig. 1). The photograph in Figure 2A shows a male Black-chinned Hummingbird with his tail spread in such a way that the base of the feathers overlapped but the tapered tips of the feathers were separated. If a male adopted a similar posture during a dive, the tips would be free to flutter while the trailing vanes of the feathers would be silenced (our videos of dives are not clear enough to reveal whether this was the case).

New insights into the natural history of birds have revealed an unappreciated diversity of nonvocal, feather-generated sounds. In many cases, the feathers responsible for mechanical sound production are oddly shaped or modified, and unique to the species. For example, the taxonomy of many species of diving hummingbirds hinges on the shape and size of the tail feathers (Stiles 1972, 1983; Graves 1986). It is now becoming clear that the unique feather shapes used by ornithologists to distinguish species could also be used by the birds to generate species-specific audio signals.

#### ACKNOWLEDGMENTS

We are indebted to Audubon California's Kern River Preserve for allowing us to work on their land, and in particular to R. Tollefson and A. Sheehy for their help. We also thank M. Denny, S. Patek, A. Prum, L. Benedict, T. Libby, R. Prum, A. Varma, P. Newsam, N. Najar, and the Center for Integrative Biomechanics Education and Research for assistance and use of equipment. Partial funding was provided by an American Museum of Natural History Chapman Grant to C.J.C. This research was approved by the University of California–Berkeley Animal Care and Use Committee and performed under C.J.C.'s scientific collecting permits. T.J.F. and C.J.C. both collected the data; T.J.F. analyzed the data and prepared the manuscript with assistance from C.J.C.

#### LITERATURE CITED

- BALTOSSER, W. H. 1987. Age, species, and sex determination of four North American hummingbirds. *North American Bird Bander* 12:151–166.
- BALTOSSER, W. H., AND S. M. RUSSELL. 2000. Black-chinned Hummingbird (*Archilochus alexandri*). In *The Birds of North America*, no. 495 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- BERTRAM, B. C. R. 1977. Variation in the wing-song of Flappet Lark. *Animal Behaviour* 25:165–170.
- BOSTWICK, K. S. 2006. Mechanisms of feather sonation in Aves: Unanticipated levels of diversity. *Acta Zoologica Sinica* 52 (Supplement):68–71.
- BOSTWICK, K. S., AND R. O. PRUM. 2003. High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *Journal of Experimental Biology* 206:3693–3706.
- BOSTWICK, K. S., AND R. O. PRUM. 2005. Courting bird sings with stridulating wing feathers. *Science* 309:736.
- BRO-JØRGENSEN, J., AND T. DABELSTEEN. 2008. Knee-clicks and visual traits indicate fighting ability in eland antelopes: Multiple messages and back-up signals. *BMC Biology* 6:47.
- CHAI, P., AND D. MILLARD. 1997. Flight and size constraints: Hovering performance of large hummingbirds under maximal loading. *Journal of Experimental Biology* 200:2757–2763.

- CLARK, C. J. 2008. Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. *Biology Letters* 4:341–344.
- CLARK, C. J., AND T. J. FEO. 2008. The Anna's Hummingbird chirps with its tail: A new mechanism of sonation in birds. *Proceedings of the Royal Society of London, Series B* 275:955–962.
- CLARK, C. J., AND T. J. FEO. 2010. Why do *Calypte* hummingbirds “sing” with both their tails and their syrinx? An apparent example of sexual sensory bias. *American Naturalist* 175:27–37.
- GRAVES, G. R. 1986. Systematics of the Gorgeted Woodstars (Aves: Trochilidae: Acestorura). *Proceedings of the Biological Society of Washington* 99:218–224.
- GREENWALT, C. H. 1960. Hummingbirds. Doubleday, New York.
- HAMILTON, W. J., III. 1965. Sun-oriented display of the Anna's Hummingbird. *Wilson Bulletin* 77:38–44.
- HARTMAN, F. A. 1961. Locomotor mechanisms of birds. *Smithsonian Miscellaneous Collections*, no. 143.
- HEDRICK, T. L., B. CHENG, AND X. DENG. 2009. Wingbeat time and the scaling of passive rotational damping in flapping flight. *Science* 324:252–255.
- HINGEE, M., AND R. MAGRATH. 2009. Flights of fear: A mechanical wing whistle sounds the alarm in a flocking bird. *Proceedings of the Royal Society of London, Series B* 276:4173–4179.
- HUNTER, T. A. 2008. On the role of wing sounds in hummingbird communication. *Auk* 125:532–541.
- HUNTER, T. A., AND J. PICMAN. 2005. Characteristics of the wing sounds of four hummingbird species that breed in Canada. *Condor* 107:570–582.
- MCGUIRE, J. A., C. C. WITT, D. L. ALTSHULER, AND J. V. REMSEN. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Systematic Biology* 56:837–856.
- MILLER, S. J., AND D. W. INOUE. 1983. Roles of the wing whistle in the territorial behaviour of male Broad-tailed Hummingbirds (*Selasphorus platycercus*). *Animal Behaviour* 31:689–700.
- NORBERG, R. Å. 1991. The Flappet Lark *Mirafra rufocinnamomea* doubles its wingbeat rate to 24 Hz in wing-clap display flight: A sexually selected feat. *Journal of Experimental Biology* 159:515–523.
- PAYNE, R. B. 1973. Wingflap dialects in the Flappet Lark *Mirafra rufocinnamomea*. *Ibis* 115:270–274.
- PYTTE, C., AND M. S. FICKEN. 1994. Aerial display sounds of the Black-Chinned Hummingbird. *Condor* 96:1088–1091.
- RANDALL, J. A. 2001. Evolution and function of drumming as communication in mammals. *American Zoologist* 41:1143–1156.
- ROME, L. C., D. A. SYME, S. HOLLINGWORTH, S. L. LINDSTEDT, AND S. M. BAYLOR. 1996. The whistle and the rattle: The design of sound producing muscles. *Proceedings of the National Academy of Sciences USA* 93:8095–8100.
- STILES, F. G. 1972. Age and sex determination in Rufous and Allen hummingbirds. *Condor* 74:25–32.
- STILES, F. G. 1983. Systematics of the southern forms of *Selasphorus* (Trochilidae). *Auk* 100:311–325.

Associate Editor: D. C. Dearborn