# Wing, tail, and vocal contributions to the complex acoustic signals of courting Calliope hummingbirds

Christopher James CLARK[1, 2*]

[1] Peabody Museum of Natural History, Yale University, PO Box 208106, New Haven, CT, 06511, USA

[2] Museum of Vertebrate Zoology, University of California- Berkeley, Berkeley, CA, USA

**Abstract**   Multi-component signals contain multiple signal parts expressed in the same physical modality. One way to identify individual components is if they are produced by different physical mechanisms. Here, I studied the mechanisms generating acoustic signals in the courtship displays of the Calliope hummingbird *Stellula calliope*. Display dives consisted of three synchronized sound elements, a high-frequency tone (*hft*), a low frequency tone (*lft*), and atonal sound pulses (*asp*), which were then followed by a frequency-modulated *fall*. Manipulating any of the rectrices (tail-feathers) of wild males impaired production of the *lft* and *asp* but not the *hft* or *fall*, which are apparently vocal. I tested the sound production capabilities of the rectrices in a wind tunnel. Single rectrices could generate the *lft* but not the *asp*, whereas multiple rectrices tested together produced sounds similar to the *asp* when they fluttered and collided with their neighbors percussively, representing a previously unknown mechanism of sound production. During the shuttle display, a trill is generated by the wings during pulses in which the wingbeat frequency is elevated to 95 Hz, 40% higher than the typical hovering wingbeat frequency. The Calliope hummingbird courtship displays include sounds produced by three independent mechanisms, and thus include a minimum of three acoustic signal components. These acoustic mechanisms have different constraints and thus potentially contain different messages. Producing multiple acoustic signals via multiple mechanisms may be a way to escape the constraints present in any single mechanism [*Current Zoology* 57 (2): 187–196, 2011].

**Keywords**   Calliope Hummingbird, Courtship, Multicomponent, Signal, Sonation, Wind Tunnel

Many signals used in animal courtship are complex (Rowe, 1999; Hebets and Papaj, 2005). Complex signals are signals containing more than one individual component. They comprise multi-modal signals, which are signals with components expressed in different sensory modalities, and multi-component signals, those in which the components are expressed in the same sensory modality (Rowe, 1999; Hebets and Papaj, 2005). There are a broad range of possible functions that complex signals may have (reviewed in Candolin, 2003; Hebets and Papaj, 2005).

Many hypotheses of function are intrinsically linked to the underlying mechanism of signal production. Every signal is limited or constrained in some way by its specific mechanism, and the limits can be biomechanical, physiological, or morphological. Different mechanisms have different constraints. Therefore, the potential information a signal contains is constrained by its mechanism, such as whether a color patch is produced via a structural color or a pigment (Hill and Montgomerie, 1994; Grether et al., 2004) or whether a communicative sound is vocally or mechanically produced (Bostwick and Zyskowski, 2001; Clark and Feo, 2010). Understanding the mechanism underlying a signal can refine the scope of possible hypotheses of that signal's function.

To examine the functional relationship between the components of a complex signal, it is necessary to identify its constituent components. This can be easy with multi-modal signals because they are produced in different physical modes (Rowe, 1999). But multi-component signals can be less clear, especially if multiple elements are produced simultaneously or in concert (Elias et al., 2006). One indication that two putative elements are different signal components is that they are produced via physically independent mechanisms. For instance, hummingbirds in the genus *Calypte* produce sounds during dive displays that acoustically match their vocal songs. Experiments show that the dive-sound is generated by the tail whereas the song is vocal, meaning that despite sounding similar they must be different signal components (Clark and Feo, 2010).

Sound may be produced by many mechanisms (Ewing 1989). In vertebrates, most research on acoustic mechanisms has focused on vocalizations in which respiratory air is internally passed through a larynx or syrinx (Goller and Larsen, 1997; Suthers and Zollinger, 2004; Gridi-Papp, 2008). Non-vocal signals, termed 'sonations' (Bostwick and Prum, 2003), are thought to be widespread (Manson- Bahr and Pye, 1985; Bostwick, 2006). In birds, recent research has identified stridulation (Bostwick and Prum, 2005), percussion (Bostwick and Prum, 2003), and resonant flutter of the flight feathers (Clark, 2008; Clark and Feo, 2008) as mechanisms of sonation.

The Calliope hummingbird *Stellula calliope* produces multiple sounds in the course of performing its courtship displays. Some of its relatives produce distinctive sounds with their tails during courtship dives, including *Calypte spp* (Clark and Feo, 2010), and the black-chinned hummingbird *Archilochus alexandri* (Feo and Clark, 2010). To dive, a male ascends high above the female (>10 m) and then swoops past her at high speed, producing species-specific tonal sound with the outer rectrix (tail-feather). Sounds are also produced by the wings in dives of Anna's and black-chinned hummingbirds (Clark, 2009; Clark and Feo, 2010). Narrowed tail-feathers create sound with the trailing vane of the feather (Clark and Feo, 2010), whereas tapered feathers generate sound with the feather's tip (Feo and Clark, 2010). The black-chinned hummingbird also produces distinctive sounds with its wings during a second courtship display, the 'shuttle' display (Feo and Clark, 2010). Shuttles are low-speed acrobatic displays performed at close range (< 1m) to the female, in which the male flies back-and-forth or simply hovers (Stiles, 1982).

As in these related species, the Calliope hummingbird performs a dive in which distinctive sounds are produced (Tamm et al., 1989; Calder and Calder, 1994). It also performs a shuttle display. But instead of narrowed, curved, or tapered feathers found in other members of this clade, Calliope hummingbird males (but not the females) have unique tail morphology. The inner rectrices are subtly spade-shaped (Williamson, 2002; Fig. 1), and all of the rectrices seem stiffened. Previous
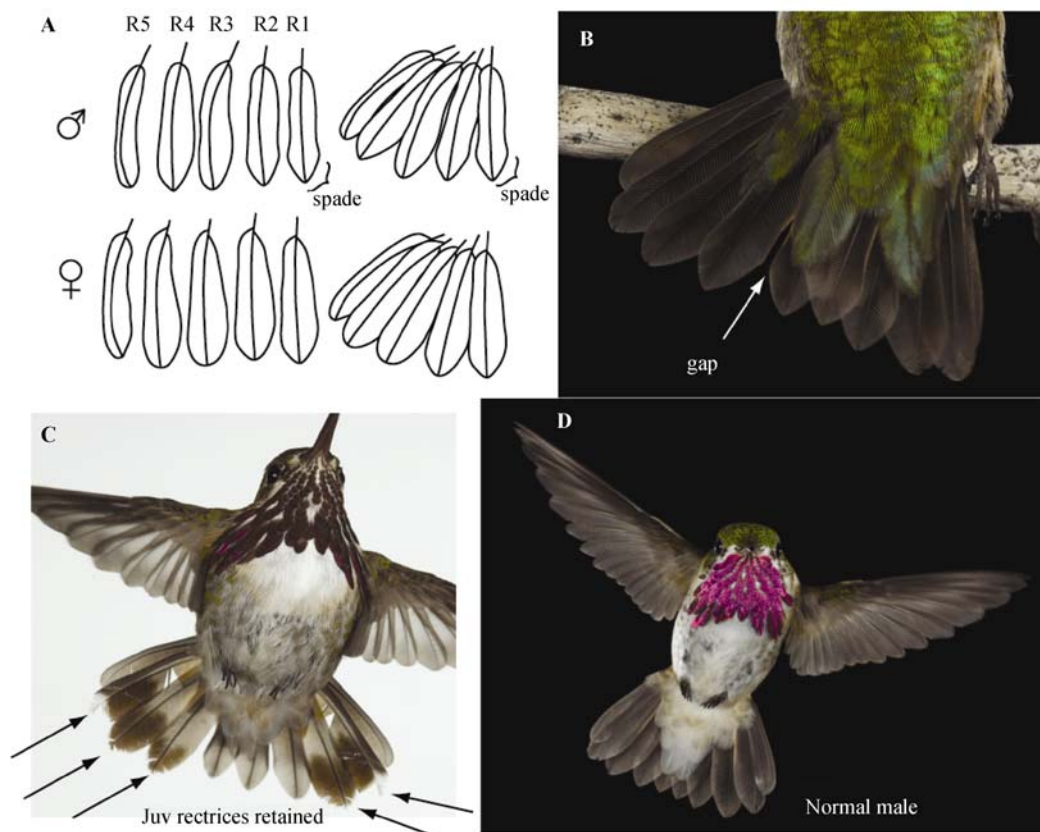


**Fig. 1    Tail morphology of adult Calliope hummingbirds (*Stellula calliope*)**
**A**. The rectrices, R1-R5 (inner to outer). Male Calliope rectrices are slightly stiffer, and the inner rectrices are subtly spade-shaped compared to females. **B**. Dorsal view of the tail. Gaps sometimes appear between the inner rectrices when birds naturally spread their tail (arrow). **C**. Adult male Calliope with five retained juvenile rectrices, as a result of an incomplete molt. **D**. An adult male Calliope with typical plumage.

work provided no *a priori* prediction as to whether or how spade-shaped tail-feathers might vibrate to produce sounds. Spectrograms of the dive-sound show it is composed of two parts produced in series: a *sputter* and a *fall* (Fig. 2), both of which are acoustically inconsistent with previously described ways in which feathers can produce sound. Specifically, the *sputter* contains atonal sound components not predicted by the resonant flutter hypothesis and dissimilar to the sounds produced by relatives, while the *fall* is frequency-modulated to a greater degree than may be possible for feather-sounds.

This paper identifies the component acoustic signals produced during courtship displays of the Calliope hummingbird. The fact that some of its relatives produce sounds with their tails during similar dives suggested that a portion of the Calliope's dive display may also be produced by the tail. Here, through high-speed video of the courtship displays, experimental manipulation of wild males, and wind-tunnel experiments, I show that the dive-sound is a complex signal comprised of both vocalizations and a previously undescribed mecha-

nism of sound production by feathers. I then discuss how the mechanisms underlying this complex signal shape its possible functions.

# 1  Materials and Methods

## 1.1  Study site

All research was approved by the UC Berkeley (2007) and Yale (2009) animal care and use committees, and conducted under California Fish & Game permit #006598 and US Fish and Wildlife Service permit MB087454-0. I studied a population of Calliope hummingbirds at UC Berkeley's Sagehen Creek Field Station, Sierra Co, California (N 39.4355°, W 120.2809°), in June and July of 2007 and 2009. In this area, male Calliope hummingbirds are locally abundant near patches of flowering food plants (*Castilleja, Arctostaphylos, Ribes spp.*) found in open areas along streams, at edges of wet meadows, and in open-canopy secondary growth. Females were not often observed on male territories, and tended to be seen in areas with greater cover. On territory, males repeatedly perched on
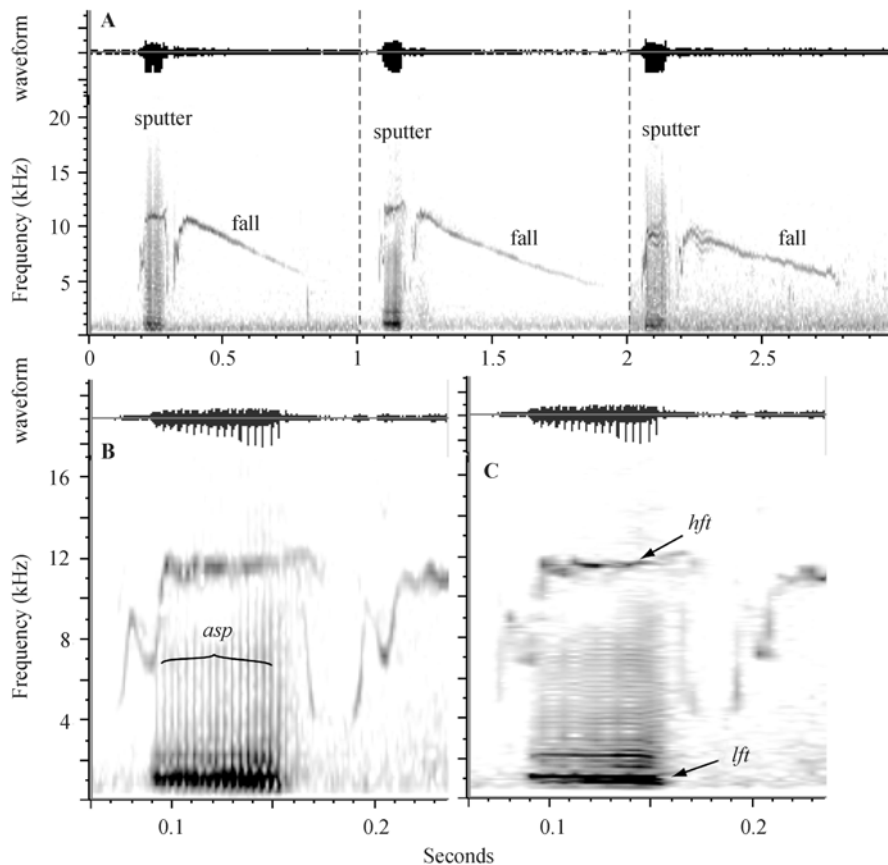


**Fig. 2   Dive-sounds of male Calliope hummingbirds**

**A**. Three example dive-sounds showing the *sputter* and *fall*. Spectrograms produced with a Hann function, 256-sample window. **B** and **C**. Identical spectrograms of the sputter, generated with a 128-sample window (B) and a 512-sample window (C). Three sound parts measured in the analyses were the frequency of the atonal sound pulses (*asp*), high frequency tone (*hft*), and the low-frequency tone (*lft*).

up to 15 individual, exposed perches, in an area approximately $30 \times 30$ m$^2$. I placed hummingbird feeders on territories to catch focal males with a feeder-trap.

Sound recordings of displays were obtained with a shotgun microphone (Sennheiser ME67, Wedemark, Germany) attached to a 16 bit digital recorder recording at 48 kHz (Marantz PMD 670, Mahwah, NJ). In 2009, high-speed videos of courtship displays were obtained at 500 or 1000 fps, $800 \times 600$ resolution with a monochrome Miro EX4 camera (Vision Research, Wayne NJ), using a c-mount 25mm f/0.95 lens (Navitar Inc, Rochester NY) or a 28-105 AF Nikkor lens f/3.5-4.5 (Nikon Inc., Melville, NY) with a c-mount to Nikon adaptor (Bower, Long Island City, NY). In addition to recording natural displays, I elicited displays (both dives and shuttle displays) by either placing a stuffed mount of a female Anna's hummingbird *Calypte anna* near one of a male's perches, placing a female Calliope in a cage on a male's territory, or by releasing a recently captured female on a male's territory.

## 1.2    Experimental manipulations and statistics

To test which rectrices were involved in producing dive-sounds, I performed experimental manipulations on wild males. First I obtained multiple recordings of dive sounds from males holding a territory, which indicated that a given unmanipulated male was capable of producing all of the parts of a typical dive-sound. After obtaining pre-manipulation dive recordings, males were caught and had one or more pairs of tail-feathers plucked to test the effect of removing those rectrices on the male's ability to produce a typical dive-sound. Each male was banded with an aluminum band and marked on the top of the head with individual patterns of liquid paper. All manipulations were bilaterally symmetrical. I then obtained recordings of post-manipulation dives from 12 of the males after they resumed territorial behavior. In the course of the experiments, I took care to be certain that the identity of a diving bird was known. Sound recordings from males where their identity was uncertain were discarded.

Individual sound elements from pre- and post-manipulation dives were scored as typical (1) or atypical (0) (i.e., weak or absent). For each sound element, the number of dives in which a typical sound element was produced after manipulation was compared to the number of typical sound elements produced by those same males before manipulation using Fisher's Exact Test.

## 1.3    Laboratory experiments

Tail-feathers from the Calliope hummingbird were tested in a wind tunnel at Yale University. The feathers

were tested in a similar fashion to Clark and Feo (2008): the feather was mounted at a realistic angle and then rotated until it began to make sound. This was performed over a range of speeds that encompass the possible flight speeds at the bottom of the dive.

The field results indicated that it was necessary to test multiple feathers together. To do this, individual rectrices were mounted to insect pins by dipping the end of the pin in cyanoacrylate glue and then inserting this end into the tip of the calamus. Sets of three neighboring tail-feathers were then glued together via these exposed pins (Fig. 3). Combinations tested were R1-R1-R2, R1-R2-R3 and R2-R3-R4. In all cases the feathers were arranged with the medial feathers lying over the dorsal surface of their lateral neighbors because this is how the feathers lie in live birds (Clark, 2010). Based on both photographs of flying birds (Fig. 1) and the high-speed videos of dives (Fig. 4), the pins were bent to angles of spread that appeared to mimic a natural angle at which the feathers might lie when the tail was spread (Fig. 3). These preparations of three feathers were then mounted in the tunnel in order to measure their sound-production capacity in aggregate. The feathers were tested at airspeeds of 22–26 m s$^{-1}$, filmed with a Miro EX4 high-speed camera at 23,121 fps, and simultaneously recorded with a microphone. As a control, the preparations were rotated to an orientation at which they did not produce sound, and a recording of the tunnel's background sound was taken. Power spectra of the background sound were subtracted from the experimental recordings (Hann, 16,384 sample window).

Lab and field sounds were analyzed using Raven 1.3 (www.birds.cornell.edu/raven) and Audacity 1.3 (audacity.sourceforge.net). Means are presented $\pm$ 1 *SD*. Sound recordings and specimens from this project have been deposited at the Museum of Vertebrate Zoology (accn #14568) and high-speed videos have been deposited in the Macaulay Library.
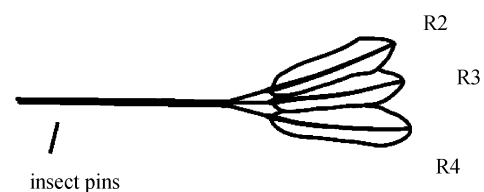


**Fig. 3    Preparation of sets of feathers tested in the wind tunnel**
An insect pin was inserted into the calamus of each the feathers, and then sets of 3 pins were glued together, such that the feathers lie in the same plane. The pins of the outer feathers were then bent to an angle that approximated the spread angle of the rectrices.
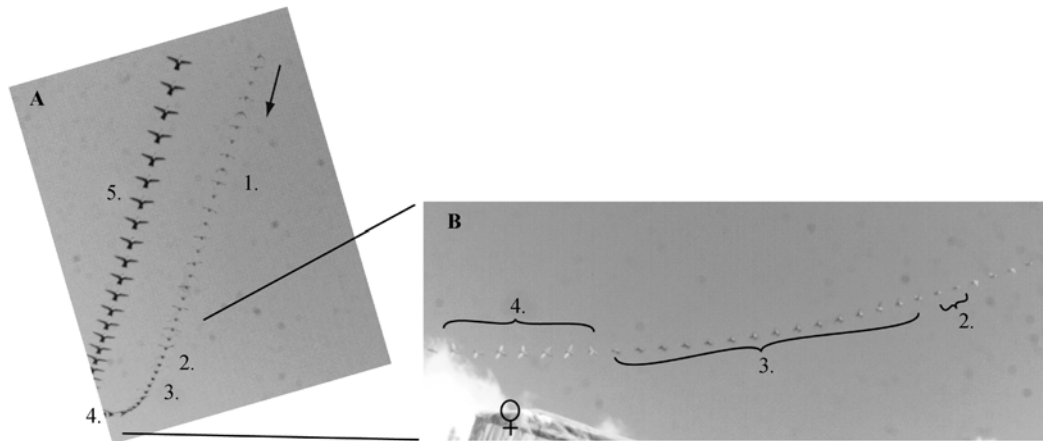
**Fig. 4   Composite images of the kinematics of the display dive of the male Calliope hummingbird**
**A**. Male diving towards the camera. Each image is 10 ms apart; the male flies out of frame during stage 4 and re-appears in stage 5. **B**. male diving from right to left, over the top of the cage holding a female. Each image is 6 ms apart. See text for further description.

## 2   Results

### 2.1   Dive and shuttle display

When a male Calliope hummingbird spotted a female on his territory he would pursue her. Females typically responded by hiding or fleeing. If the male caught up with a fleeing female, she would descend and land in a bush or tree on the male's territory. Often, the female landed inside thick foliage such that dives were likely visually occluded. To these perched females, males would perform either shuttle displays, a bout of dives (5.7 ± 6.4 dives per bout, range: 1–34), or both. Shuttle displays typically preceded bouts of dives.

Sixteen high-speed videos of display dives were obtained from nine individual males. Each video showed a unique fragment of the kinematic sequence of a dive, but by comparing various videos stereotypical dive stages could be identified (Fig. 4). Initially (stage 1), the birds descended, flapping their wings at 70 ± 3.5 hz ($n$ = 7 videos). By the end of stage 1 they had pulled up and were approaching the bottom of the dive and transitioned into a glide. This glide (stage 2) was brief, lasting 18 ± 8.2 ms ($n$ = 6 videos), then while continuing the glide, the birds spread their tails, and glided with it spread, for 73 ± 14 ms ($n$ = 5 videos; stage 3). The tail did not seem to be completely spread during this stage. At the start of stage 4, the birds abruptly executed a roll of approximately 90° (Fig. 4b), such that one wing pointed straight up, and the other straight down as they glided over the target of the display. The roll lasted for 83 ± 23 ms ($n$ = 6 videos), and it appeared that the tail was shut at some point during the roll, though none of the videos were sufficiently clear to determine precisely

when this occurred. Stage 5 then occurred as the birds gradually rolled back to upright as they continued to glide. At this point they had passed over the female and were ascending, either to begin another dive or to transition to another behavior. Males flew over the female at the start of stage 4 and typically passed within 1 m of the female.

Five high-speed videos were obtained of three individual males performing shuttle displays to stuffed mounts. One of these videos can be seen on YouTube (www.youtube.com/watch?v =UXrz 2Igd07c). During the display, males erected their gorget (Fig. 5) and hovered in front of the mount while producing a loud buzzing sound. In related species, the shuttle display includes significant lateral (side-to-side) motions, but these motions were nearly absent in the Calliope's shuttle. In three videos the males hovered without obviously modulating their wingbeat frequency, while in two other shuttle displays, while hovering in place, the birds modulated their wingbeat frequency, flapping their wings in pulses. Each pulse lasted for six to 15 wingbeats at a wingbeat frequency of 94.8 ± 2.3 Hz ($n$ = 9 bouts), followed by a pause in which the wings were flapped at a lower frequency. This represents a 42% increase in wingbeat frequency, compared to a hovering wingbeat frequency of 66.5 Hz reported for males (Hunter and Picman, 2005). The longest that a male continuously performed a shuttle display was 24 s, though bouts tended to be shorter. Loud buzzing sounds were also produced by the wings during these displays (Fig. 6); the sound pulses of the shuttle display were produced at a rate of 92.7 ± 5.9 Hz ($n$ = 20 sound recordings from 11 males; range = 1–3 recordings per male).

**Fig. 5   Male Calliope performing a natural shuttle display to a female**
During the display, the wingbeat frequency is elevated in pulses that create a buzzing sound. The female is often perched while the male performs this display.
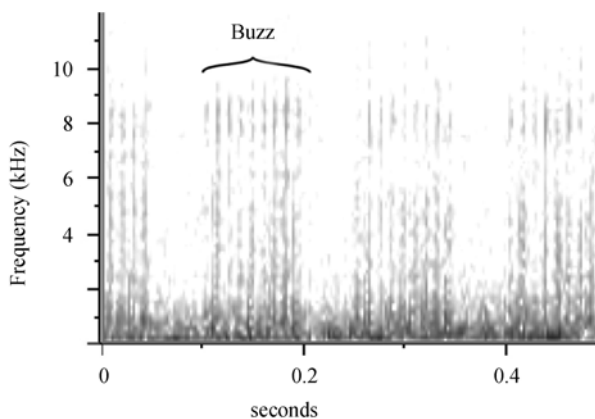


**Fig. 6   Spectrogram of the buzzing sound produced during the shuttle display**
Each pulse of sound is produced by a rapid burst of wingbeats. Hann, 256 sample window.

## 2.2   Dive sounds of normal males

I observed several hundred dives from >30 adult male Calliope hummingbirds. Of these, 12 males underwent manipulations and were successfully recorded again after manipulation. They produced a cumulative total of 142 dives prior to manipulation. These 12 males produced typical dive sounds; one additional unmanipulated but atypical male is described below. In some dives, sounds were present but could not be further quantified due to background sounds (e.g., song of other birds), hence some sample sizes below are less than 142. While diving, male Calliope hummingbirds emitted a dive-sound comprised of two distinctive components: the *sputter* and the *fall* (Fig. 2). A typical *sputter* had three acoustic components, one of which was a high frequency, frequency-modulated tone, *hft* (high-frequency tone). The frequency of the *hft* began at around 5 kHz, rapidly fluctuated up and down before reaching a peak, stable frequency of $10.88 \pm 0.61$ kHz ($n = 137$). The second component of the sound was a low-frequency tone (*lft*) with an acoustic frequency of $1.02 \pm 0.19$ kHz ($n = 126$) that did not appreciably vary in frequency, and lasted $67 \pm 6$ ms ($n = 125$). The third component of the *sputter* were a series of atonal (broadband) sound pulses (*asp*), that appeared at a pulse rate of $238 \pm 20.6$ Hz ($n = 120$). The sputter contained more acoustic energy than did the fall (Fig. 2).

The *fall* was produced in 120 of 142 dives of normal males (84.5 % of all dives). It consisted of a single, frequency-modulated tone that began at around 5 kHz, was rapidly modulated up to a peak frequency of $10.3 \pm 0.54$ kHz ($n = 120$), and then gradually descended in frequency over a duration of $0.60 \pm 0.11$ sec (Fig. 2).

## 2.3   Dive sounds of a male with juvenile rectrices

One unmanipulated male provided an exception to the patterns described above. He performed 13 natural dives but never produced a typical *sputter* during a dive (Table 1): in all 13 dives the low-frequency tone was scored as weak (quiet) ($n = 9$) or absent ($n = 4$). Moreover, the *asp* were only present in two of 13 dives, whereas the *hft* and *fall* were present in all dives (Fig. 7). He had most of the plumage and behaviors of an adult male Calliope, but when captured, he was found to have retained five juvenile rectrices: right R2, R3, R4, and left R3 and R4 (Fig. 1). This male was photographed,

**Table 1    Effects of experimental manipulation on production of components of the dive sound**

| Component | N (birds) | hft | | lft | | asp | | fall | | n (dives) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Manipulation | | pre | post | pre | post | pre | post | pre | post | pre | post |
| Pluck all rectrices | 1 | 100% | 100% | 100% | 0%* | 100% | 0%* | 100% | 100% | 6 | 7 |
| Pluck R1/ R2/ R3/ R4 | 1 | 100% | 100% | 100% | 0 %* a | 100% | 0% * | 100% | 100% | 3 | 11 |
| Pluck R1 | 3 | 94% | 97% | 94% | 56% * a | 89% | 78% a | 92% | 90% | 36 | 32 |
| Pluck R2/ R3 | 3 | 97% | 86% | 84% | 0% * a | 95% | 0%* | 63% | 91% | 38 | 22 |
| Pluck R4/ R5 | 2 | 96% | 100% | 96% | 8%* | 84% | 0%* | 98% | 69% | 45 | 23 |
| Pluck R5 | 2 | 100% | 71% | 92% | 57%a | 84% | 64%a | 76% | 21% | 13 | 14 |
| Juv rectrices naturally retained | 1 | n/a | 54% | n/a | 0% a | n/a | 15% | n/a | 100% | n/a | 13 |

* Statistically significant reduction (Fisher's Exact Test, *P* < 0.05). ᵃ Some atypical dives still had some sound present (e.g. Fig. 7).
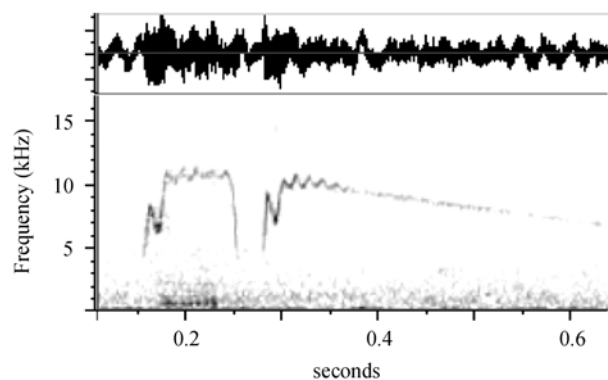Percentages are the number of typical dive sounds out of the total number of dives (*n*).



**Fig. 7    Atypical dive-sound recording of an unmanipulated male that naturally retained juvenile rectrices**
The *lft* is faint and the *asp* are absent.

collected and deposited in the Museum of Vertebrate Zoology (MVZ; #183701). The male was collected as a voucher for this study and as reference material for future researchers.

## 2.4    Experimental manipulations of wild birds

Results of all experimental manipulations are presented in Table 1, and the most salient results are as follows. I plucked all ten rectrices of one male: he was still able to produce the *fall* portion of his dive-sound, as well as the *hft* of the *sputter*, unambiguously indicating that these must not be produced by the tail. By contrast, after manipulation he never produced the *lft* or the *asp* portions of the *sputter*, suggesting that these sounds may be tail-generated.

Other birds had various combinations of tail-feathers manipulated (see Table 1), and while plucking different tail-feathers tended to cause a statistically significant reduction in the production of *lft*, under any specific manipulation the sound was still present to some degree during some dives. Likewise, production of the *asp* was reduced by most of the manipulations, but notably, the manipulation of exclusive sets of feathers (e.g. removing R4 and R5 versus removing R2 and R3) had essentially the same experimental effect (see Table 1). Altogether, these results suggest no single feather is critical for production of the *lft* and *asp*, instead suggesting that the *lft* and *asp* are produced by multiple rectrices.

## 2.5    Wind tunnel experiments

Isolated Calliope rectrices (R1 through R5) placed in a wind tunnel could be made to flutter. The fundamental frequency of the fluttering motion was typically ~0.5 kHz, but the dominant frequency of sounds that resulted was normally the second harmonic of 1.0 to 1.3 kHz, matching the *lft* (Fig. 8B). The sounds that single feathers produced tended to be weak, and sometimes they fluttered wildly while not producing any sound detectable above the background sound of the tunnel. No individual feather placed in the wind tunnel produced sounds similar to the *asp*.

To test the hypothesis that the *asp* was produced by feather-feather interactions, I experimented with nine different sets of three feathers. The results were similar for all of the sets of feathers independent of which rectrices were used, so the results for all sets are combined. By orienting the feathers so that they overlapped slightly, it was possible to get the rectrices to flutter and hit each other (Fig. 3). A supplemental high-speed video of the feathers fluttering and colliding can be found on YouTube (www.youtube.com/watch?v=265VdJRebzg&NR =1).

The feather sets fluttered at an average frequency of 0.469 ± 0.037 kHz (*n* = 9). Of the sounds produced by the fluttering feathers, five exhibited a fundamental frequency matching the flutter frequency (~0.47 kHz) and a series of higher odd and even harmonics. Three were instead missing the fundamental frequency, and the 2nd harmonic of approximately 0.9 kHz was dominant

(Fig. 8 A–C). The final set did not produce tones distinguishable from the high levels of background sound. Moreover, all nine sets exhibited an increase in atonal sound generated by the collisions, relative to control recordings (Fig. 8C).

### 2.6   Synthesis: a new mechanism of sonation

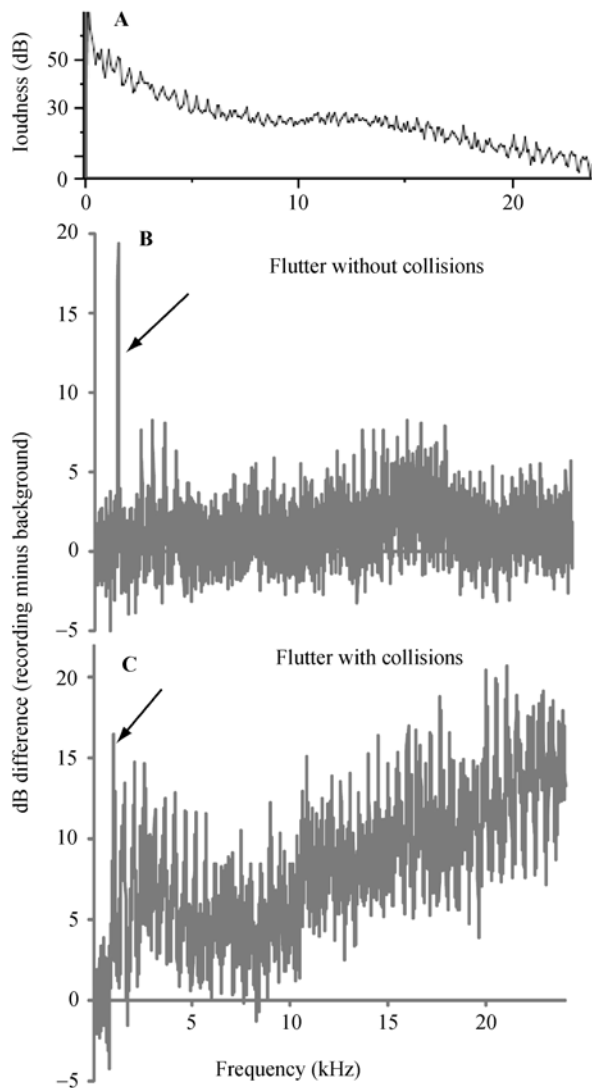The wind tunnel experiments and manipulative experiments on wild Calliope hummingbirds suggest that



**Fig. 8   Power spectra of sounds made by Calliope feathers in a wind tunnel (Hann, 16, 384 samples)**

**A**. Raw power spectrum of a set of calliope feathers fluttering and colliding with each other in the wind tunnel, including background sound; dB are arbitrary. B and C Power spectra of feathers in the wind tunnel with the power spectrum of the background sound subtracted. **B**. Calliope rectrix fluttering but not hitting its neighbors. The dominant frequency (arrow) is the 2nd harmonic of the fluttering motion. **C**. Calliope rectrices fluttering and striking each other. The dominant frequency (arrow) is approximately the same as in B, but many harmonics are stonger, as is an overall increase in atonal sound energy at higher frequencies.

the *lft* and *asp* portions of the dive-sound are generated by the tail-feathers. In particular, the field manipulations suggested that all the rectrices are involved in the production of the *lft* and *asp* (Table 1). The dive kinematics were consistent with this hypothesis: high-speed videos of dives indicated that when the male spreads his tail at the bottom of the dive, the time that the tail is spread (73 ms) matched the length of the *sputter* (67 ms). Moreover, the tail was not spread as widely as other species (pers obvs), such that the rectrices appeared to be close enough to collide as they flutter (Fig. 4).

The lab experiments suggested that a significant portion of the sound is generated by collisions between the rectrices. In the wind tunnel, all the rectrices (R1-R5) fluttered at frequencies of ~0.5 kHz, while the dominant sound frequency corresponding to the flutter was the second harmonic of ~1.0 kHz (Fig. 8), matching the frequency of the *lft* (Fig. 2). The atonality and harmonic structure of the *asp* of diving birds was not replicated by any individual feather. Rather it was similar to the sounds generated when multiple rectrices collided with each other in the wind tunnel (compare Fig. 2 to Fig. 8). In wild birds, the pulse rate of the *asp* was ~0.25 kHz. This suggests that as the rectrices flutter at 0.5 kHz, they strike each other every other cycle. In the lab preparations, the feathers appeared to hit each other every cycle, but this was likely caused by the lab preparation failing to mimic some aspect of the orientation of the feathers, such as that only three feathers were included rather than all 10.

The manipulations of wild birds show that the *hft* and *fall* of the dive display were not produced by the tail (Table 1), and as their frequency modulation is not consistent with any known wing sonation, I hypothesize they are produced vocally. During the shuttle display, the trill rate of the buzzing sounds (93 Hz) corresponded to the wingbeat frequency (95 Hz), indicating that the buzzing sounds are generated by the wings.

## 3   Discussion

Evidence suggests that both the wing sounds and the tail sounds are courtship signals, rather than cues incidentally arising from visual flight displays. Both the wing and tail-generated sounds identified in this study are relatively loud, e.g. the tail-generated portions of the *sputter* are louder than the vocal *fall* (see waveform in Fig. 2). The tail morphology is sexually dimorphic with the male alone having stiffened, spade-shaped tail feathers (Fig. 1). Their mode of flutter appears to be unique (Clark unpublished), and I hypothesize their

shape and stiffness facilitate their fluttering to hit each other. Calliope is nested inside of *Selasphorus* (McGuire et al., 2009) and the feather-feather percussion described here is not found in any of its sister taxa (Clark unpublished), thus the *sputter* of the dive-sound is a recently evolved, derived character solely found in the courtship display of this species. Females experiencing the display often perch deep inside a bush or tree where any visual effects of the dive may be marginal. Finally, whereas some relatives (sheartails) do spread and present the tail to females in a way suggesting it is a visual signal (Clark unpublished), the Calliope has no similar behaviors that suggest its tail also serves as a visual signal.

The wing-generated buzzes of the shuttle display are also likely to be a signal. Wing hum is an acoustic expression of the wingbeat frequency (Hunter and Picman, 2005; Hunter, 2008) and is an intrinsic byproduct of flight. It is therefore not likely to be a signal. Wing trills (such as the buzz), by contrast, are not an intrinsic byproduct of flight and are produced predominantly by males, as is the case in the Calliope hummingbird. Hunter (2008) performed extensive playback experiments in an aggressive context to show that female Calliope hummingbirds respond to hovering sounds of other hummingbirds, including the trill of male Calliope, and concluded that the trill was a signal. The wing trill males produce during the shuttle display (Fig. 6) is far louder than the hovering sounds Hunter (2008) used in his experiments (Clark pers obvs), thus it is likely a signal.

The dive includes multicomponent sounds in which the *lft* and *asp* together comprise one component produced by the cumulative action of the rectrices fluttering and striking each other. Simultaneously, the birds vocally produced the *hft*, followed by the *fall*. The shuttle display appears to comprise a multimodal signal consisting of the spread gorget (Fig. 5) and sounds produced by the wings (Fig. 6). Ultimately, functions that could be ascribed to these sounds (such as an indicator of quality) will be mechanism-specific. Each of the three distinct sound-producing mechanisms demonstrated here has unique constraints.

For instance, producing the tail-sound requires the correct (adult) feathers, as illustrated by the abnormal Calliope that retained juvenile rectrices (Fig. 1C) and failed to produce a typical dive-sound (Fig. 7). Hummingbirds occasionally fail to undergo complete molt, retaining flight feathers from the previous year (Pyle et al., 1997). This may happen especially to hatch-year birds, which tend to initiate molt later than older birds

(Pyle, 2001; Williamson, 2002). Similarly, in a population of Costa's hummingbirds, one individual had a naturally malformed rectrix, and failed to produce a typical dive-sound in half of his dives (Clark and Feo, 2010). These demonstrations of dramatic natural variation in feather condition and sound production suggest the hypothesis that the display could indicate the male's ability to grow normal tail-feathers during the annual molt. Aspects of the dive sound (e.g., loudness) are functionally connected to dive behavior (e.g., dive speed) so the sound might serve as an indicator of a bird's ability to dive. At this point, these hypotheses of function have not been tested against the null hypothesis that female preference for these traits is arbitrary (Prum, 2010).

In contrast to tail-sounds, the buzzing wing sounds of the shuttle are produced cyclically with each wingbeat, and are thus intrinsically linked to males' flight performance during display. The performance itself is notable, as the males increased wingbeat frequency to ~95 Hz, ~40% above hovering wingbeat frequency, for up to 25 s (Tamm et al., 1989, this study). Muscles have intrinsic limits in their ability to generate high-frequency contractions (Altshuler et al., 2010), so this display is likely near the performance limits of their large flight muscles, having been pushed there by female preference (Clark, 2009). Possibly, the temporal frequency or loudness of the buzzing sound could serve as a signal of a male's flight capacity. The null hypothesis is that females arbitrarily favor the sounds made by the wings, and so males have been pushed to an arbitrary flight performance limit by this directional preference (Prum, 2010).

During the dive the males coordinate production of both the tail-sound and a vocalization to produce an integrated sound. This is similar to the displays of wolf spiders, which produce a multicomponent acoustic/vibratory signal, with different acoustic components produced via independent mechanisms (Elias et al., 2006). The simultaneous multicomponent acoustic display are analogous to individual multicomponent color patches described in fish (Grether et al., 2004; Svensson et al., 2008). Specifically, Grether et al. (2004) argue a single color patch can be multicomponent because independent biophysical mechanisms (such as both carotenoids and chromatophores) simultaneously contribute to the overall color of a single patch (Grether et al., 2004; Svensson et al., 2008). Females may have preferences for signals that males cannot match as effectively using just one mechanism, such that combining two mechanisms to produce an integrated signal may be a

way of escaping this constraint. In other words, the co-ordinated presentation of simultaneous vocalizations and sonations increases the range of possible sounds a male can produce.

# References

Altshuler DL, Welch KC, Cho BH, Welch DB, Lin AF et al., 2010. Neuromuscular control of wingbeat kinematics in Anna's hummingbirds *Calypte anna*. Journal of Experimental Biology 213: 2507–2514.

Bostwick K, Zyskowski K, 2001. Mechanical sounds and sexual dimorphism in the crested doradito. Condor 103: 861–865.

Bostwick KS, 2006. Mechanisms of feather sonation in Aves: Unanticipated levels of diversity. Acta Zoologica Sinica 52S: 68–71.

Bostwick KS, Prum RO, 2003. High- speed video analysis of wing- snapping in two manakin clades (Pipridae: Aves). Journal of Experimental Biology 206: 3693–3706.

Bostwick KS, Prum RO, 2005. Courting bird sings with stridulating wing feathers. Science 309: 736.

Calder WA, Calder LL, 1994. Calliope Hummingbird. In: Poole A, ed. Birds of North America 135. Ithaca, NY: Cornell Lab of Ornithology

Candolin U, 2003. The use of multiple cues in mate choice. Biological Reviews 78: 575–595.

Clark CJ, 2008. Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. Biology Letters 4:341–344.

Clark CJ, 2009. Courtship dives of Anna's hummingbird offer insights into flight performance limits. Proceedings of the Royal Society of London B 276: 3047–3052.

Clark CJ, 2010. The evolution of tail shape in hummingbirds. Auk 127: 44–56.

Clark CJ, Feo TJ, 2008. The Anna's Hummingbird chirps with its tail: A new mechanism of sonation in birds. Proceedings of the Royal Society of London B 275: 955–962.

Clark CJ, Feo TJ, 2010. Why do *Calypte* hummingbirds "sing" with both their tail and their syrinx? An apparent example of sexual sensory bias. American Naturalist 175: 27–37.

Elias DO, Lee N, Hebets EA, Mason AC, 2006. Seismic signal production in a wolf spider: Parallel *versus* serial multi- component signals. Journal of Experimental Biology 209: 1074–1084.

Ewing AW, 1989. Arthropod Bioacoustics Neurobiology and Behaviour. Ithaca: Cornell University Press.

Feo TJ, Clark CJ, 2010. The displays and sonations of the black-chinned hummingbird (Trochilidae: *Archilochus alexandri*). Auk 127: 787–796.

Goller F, Larsen ON, 1997. *In situ* biomechanics of the syrinx and sound generation in pigeons. Journal of Experimental Biology 200: 2165–2176.

Grether GF, Kolluru GR, Nersissian K, 2004. Individual colour patches as multicomponent signals. Biological Reviews 79: 583–610.

Gridi-Papp M, 2008. The structure of vocal sounds produced with the mouth closed or with the mouth open in treefrogs. Journal of the Acoustical Society of America 123: 2895–2902.

Hebets EA, Papaj DR, 2005. Complex signal function: Developing a framework of testable hypotheses. Behavioral Ecology and Sociobiology 57: 197–214.

Hill GE, Montgomerie R, 1994. Plumage colour signals nutritional condition in the house finch. Proceedings of the Royal Society of London B 258: 47–52.

Hunter TA, 2008. On the role of wing sounds in hummingbird communication. Auk 125: 532–541.

Hunter TA, Picman J, 2005. Characteristics of the wing sounds of four hummingbird species that breed in Canada. Condor 107: 570–582.

Manson-Bahr PH, Pye JD, 1985. Mechanical Sounds. In: Campbell B, Lack E ed. Dictionary of Birds. Vermillion: Buteo Books.

McGuire JA, Witt CC, Remsen JV, Dudley R, Altshuler DL, 2009. A higher- level taxonomy for hummingbirds. Journal of Ornithology 150: 155–165.

Prum RO, 2010. The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. Evolution 64: 3085–3100.

Pyle P, 2001. Identification Guide to North American Birds. Part 1. Columbidae to Ploceidae. Bolinas: Slate Creek Press.

Pyle P, Howell SNG, Yanega GM, 1997. Molt, retained flight feathers and age in North American hummingbirds. In: Dickerman RW ed. The Era of Allan R. Phillips: A Festschrift. Albuquerque: Horizon Communications, 155–166.

Rowe C, 1999. Receiver psychology and the evolution of multicomponent signals. Animal Behaviour 58: 921–931.

Stiles FG, 1982. Aggressive and courtship displays of the male Anna's hummingbird. Condor 84: 208– 25.

Suthers RA, Zollinger SA, 2004. Producing song the vocal apparatus. Annals of the New York Academy of Science 1016: 109–129.

Svensson PA, Pélabon C, Blound JD, Forsgren E, Bjerkeng B et al., 2008. Temporal variability in a multicomponent trait: Nuptial coloration of female two-spotted gobies. Behavioral Ecology 20: 346–353.

Tamm S, Armstrong DP, Tooze ZJ, 1989. Display behavior of male Calliope hummingbirds during the breeding season. Condor 91: 272–279.

Williamson SL, 2002. Hummingbirds of North America. New York: Houghton Mifflin Company.