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Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds

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Sounds produced continuously during flight potentially play important roles in avian communication, but the mechanisms underlying these sounds have received little attention. Adult male Red-billed Streamertail hummingbirds (*Trochilus polytmus*) bear elongated tail streamers and produce a distinctive 'whirring' flight sound, whereas subadult males and females do not. The production of this sound, which is a pulsed tone with a mean frequency of 858 Hz, has been attributed to these distinctive tail streamers. However, tail-less streamertails can still produce the flight sound. Three lines of evidence implicate the wings instead. First, it is pulsed in synchrony with the 29 Hz wingbeat frequency. Second, a high-speed video showed that primary feather eight (P8) bends during each downstroke, creating a gap between P8 and primary feather nine (P9). Manipulating either P8 or P9 reduced the production of the flight sound. Third, laboratory experiments indicated that both P8 and P9 can produce tones over a range of 700–900 Hz. The wings therefore produce the distinctive flight sound, enabled via subtle morphological changes to the structure of P8 and P9.

Keywords: Red-billed Streamertail; hummingbird; sonation; mechanical sound; feather; tail

1. INTRODUCTION

Many birds produce tonal flight sounds that are attributed to air flowing over or through the wings or tail (Bahr 1907; Bostwick 2006; Clark & Feo 2008). Four complementary lines of evidence suggest that these sounds are not vocal: (i) production only during a particular mode of flight, (ii) experimental elimination of sound production in live birds (Miller & Inouye 1983), (iii) experimental reproduction of flight sounds using isolated feathers (Bahr 1907; Carr-Lewty 1943; Reddig 1978), and (iv) inference of feather function based on an unusual shape. For instance, male Red-billed Streamertails (*Trochilus polytmus*; hereafter, streamertails) have greatly elongated fourth tail feathers (hereafter, streamers) and make a distinctive 'whirring' sound during various modes of flight (hereafter, the flight sound). Females and subadult males lack streamers and do not make the flight sound, causing ornithologists to attribute the production of the flight sound to the male's streamers (Allen 1961; Bond 1961; Downer & Sutton 1990; Tyrrell & Tyrrell 1990; Evans *et al.* 1994; Schuchmann 1999; Raffaele *et al.* 2003). However, inferences based on feather shape alone can be misleading. Here, I show that the tail streamers do not produce the sound; it is actually produced by the primary feathers eight (P8) and nine (P9) wing feathers (figure 1*a*).

2. MATERIAL AND METHODS

I conducted fieldwork near Hardwar Gap (18.0899° N, 076.6990° W) from 24 July to 16 August 2004 and 15 June to 13 July 2005. This is the beginning of the annual moult of the local streamertails, which are endemic to Jamaica. Because some wild birds were missing their streamers or pairs of wing feathers, the annual moult provided a natural experiment to test which feathers produce the flight sound.

In addition to observing natural variation in wild birds, I captured males and placed them in a $2.5\times2.5\times1.5\ \mathrm{m}^3$ flight arena with perches and a feeder. Individuals were allowed to feed and preen their flight feathers, then hovering flight was filmed at the feeder with a high-speed camera, at 500 or 1000 fps (Redlake MotionMeter).

The ability to produce the flight sound was classified into three categories: strong (produced continuously during flight, including hovering flight); weak (faint, not produced continuously and not during hovering flight); and absent (I never heard the bird produce the sound). The sound seemed loudest when the birds manoeuvred, so I stimulated manoeuvres by chasing them within the large arena for at least 30 s. Sound production during this time was assessed by ear. Birds that initially produced strong flight sounds were subjected to one of three experimental treatments: streamers removed; P8 removed; or P9 removed. Following manipulation, individuals were allowed a minimum of 30 min to rest and preen, and flight sound production was again assessed. Some flight sounds were recorded by the microphone of a Sony DCR-TRV19 DV camcorder, extracted as .WAV files using FINAL CUT PRO v. 5.0.2 and visualized using RAVEN v. 1.3.1 (Charif *et al.* 2007).

Because birds were released into the wild at the conclusion of the study, only two wing feathers (one per wing) could be manipulated on each bird, to prevent flight from being unduly impaired. P8 or P9 was clipped if a bird would soon moult the feather, or plucked if the feather was fresh and, if clipped, would potentially not be moulted for a full year.

P8 and P9 were tested for the capacity to produce the flight sounds using the protocols described in Clark & Feo (2008). Briefly, the feathers were placed in a jet of air, and orientation was manipulated until they began producing sound. This allowed simultaneous filming with a high-speed camera recording 30 000 fps, and sound recording with a Sennheiser ME-67 microphone attached to a 16-bit digital recorder sampling at 48 kHz (Marantz PMD 670). The feathers were also placed in a wind tunnel, allowing recordings of sounds produced by the feathers over a range of airspeeds.

3. RESULTS

Observations of wild birds and experiments indicated that 15 male streamertails made strong flight sounds while missing their streamers. By contrast, removing either P8 or P9 reduced the flight sound to weak or absent after manipulation, in all individuals tested (P8, $n=3$; P9, $n=4$).

Hovering male streamertails had a wingbeat frequency of 28.8 ± 1.84 Hz ($n\pm$s.d.; $n=11$ videos from four birds). At the start of the downstroke, a gap appeared between P8 and P9 caused by the bending of P8 (figure 1*c*). This gap persisted for the duration of the downstroke (frames 12–27 of figure 1*c*), and did not occur during the upstroke (especially evident in frames 7–10 of figure 1*c*). High-speed videos indicated that females and subadult males did not exhibit this same gap during the downstroke (figure 1*b*), and the flight sound was absent.

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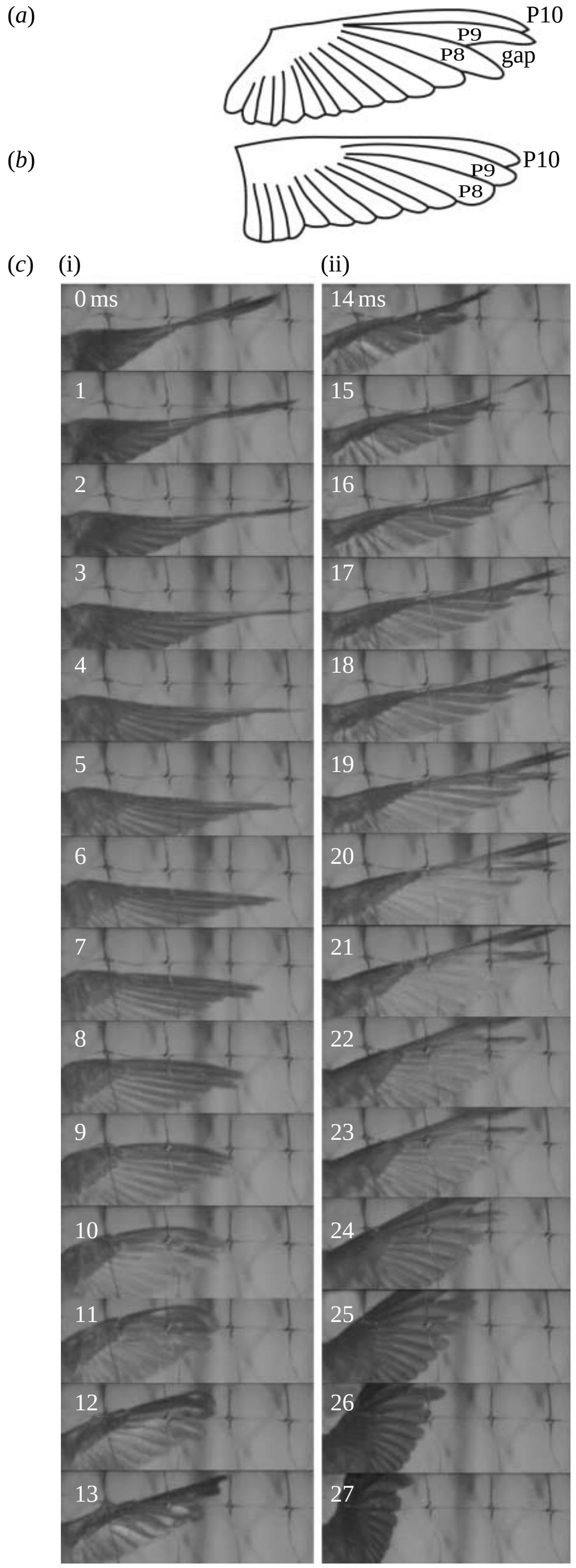

Figure 1. (*a*) Adult male streamertail's wing during the mid-downstroke, traced from a high-speed video. (*b*) Subadult male streamertail's wing during the mid-downstroke, traced from a high-speed video. (*c*) Images from the downstroke (i) and upstroke (ii) of a male streamertail's wingbeat. Consecutive images are 1 ms apart. P8, P9 and P10 bend during wing pronation (frames 10–13), resulting in a gap between P8 and P9 during the downstroke, which is absent in the upstroke.

The flight sound was produced in pulses at a rate of 28.5 ± 1.81 pulses s^{-1} ($n \pm$ s.d.; $n=9$ recordings; figure 2*a*). This was not significantly different from the wingbeat frequency (*t*-test, $p>0.2$). Each pulse was a tonal sound with a mean fundamental frequency of 858 ± 53 Hz ($n \pm$ s.d.; $n=9$ sound recordings; figure 2*a*).

Placing P9 in the jet of air produced tones with a fundamental frequency of 907 ± 34.7 Hz ($n=6$ feathers; figure 2*b*), marginally different from the flight sound (*t*-test, $n=15$, $p=0.07$), while P8 feathers produced tones of 1090 ± 31 Hz ($n=4$ feathers), significantly different from the flight sound (*t*-test, $n=13$, $p<0.001$). Only the feather's tip produced these sounds. High-speed videos indicated that the feather's tip fluttered up and down at the same frequency as the sound (figure 2*c*,*d*). When placed in a wind tunnel, both P8 and P9 exhibited nearly identical frequency–velocity curves, producing sounds ranging from below 700 Hz to above 850 Hz (figure 2*e*). In both the jet and the wind tunnel experiments, the sounds from P9 seemed louder and easier to elicit than those from P8.

4. DISCUSSION

Tail-less male streamertails could produce the flight sound, indicating that it is not generated by the tail. Three lines of evidence suggest that wing feathers P8 and P9 produce the flight sound. First, the manipulation of either P8 or P9 impaired (but did not completely eliminate) the ability to produce the flight sound. Second, high-speed videos suggest a mechanism: the P8 bends during the downstroke of each wingbeat, forming a gap between P8 and P9. Consistent with this, the hovering wingbeat frequency matches the pulse frequency of the flight sound. The gap frees the tip of P9 from contact with P8, potentially allowing either to flutter. Laboratory experiments indicate that both the tips of P8 and P9 can flutter, producing sound at the frequency of the flight sound (figure 2*b*,*e*).

The experiments on live birds suggest that both P8 and P9 are necessary for the sound to be produced consistently and loudly. When either was missing, the flight sound was faint and irregularly produced, and was presumably produced solely by the remaining feather, or possibly by P10 when it was uncovered and free to flutter by the absence of P9. So, in unmanipulated birds, the loudness and consistency of production of the sound may result from both P8 and P9 simultaneously and independently fluttering to produce the sound. However, this does not explain why sound production was absent in some of the manipulated birds; this detail suggests that the neighbouring feathers may interact.

The laboratory experiments suggest that the mechanism producing the flight sound of the red-billed streamertail is similar to the Anna's Hummingbird, which produces sound when the trailing edge of a tail feather flutters at its resonant frequency (Clark & Feo 2008). As a result, the sound's tone will be set by the shape of the feather, with smaller or more emarginated feathers producing higher frequencies (Clark *et al.* in preparation). The tone's frequency varies little with air velocity (figure 2*e*), meaning that the sound's frequency will change little as the wingtip velocity

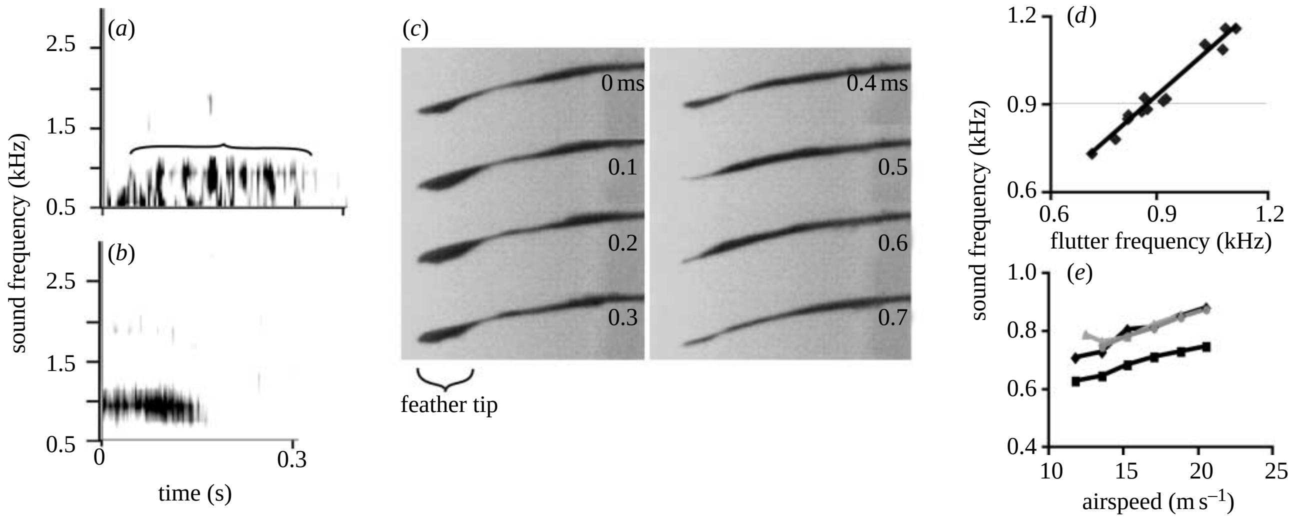

Figure 2. (*a*) Spectrogram of the flight sound of a caged adult male Red-billed Streamertail, over seven wingbeats. Most sound below 650 Hz is background noise. (*b*) Spectrogram of the sound produced by an isolated P9 in a jet of air, at the same frequency as the flight sound. (*c*) Consecutive images of P9 projecting into a stream of air (0.1 ms apart), exhibiting the fluttering of the tip. (*d*) Flutter and sound frequencies correspond perfectly (regression, slope = 1.04, $r^2 = 0.97$). (*e*) Feather frequency as a function of air velocity in a wind tunnel. Black, P9 ($n=2$); grey, P8 ($n=2$); the three lines are coincident.

changes with varying modes of flight such as hovering versus manoeuvring versus fast forward flight. The air velocity may affect the sound's loudness, however, as suggested by the observation that the sound seemed louder when the birds manoeuvred in the flight arena, or when wild birds flew by at high speed.

Observers inferred that this unusual sound was tail generated because streamers are an obvious morphological feature unique to adult males, whereas unique features of males' wing feathers are subtle. In some cases, the morphological features associated with sound production may be apparent, such as in male broad-tailed hummingbirds. These also produce a flight sound, and P10 is narrow, forming a gap observable in the wings of museum specimens. Experiments confirmed that the gap produces the flight sound (Miller & Inouye 1983). By contrast, streamertails in the hand have no such gap; the gap is only apparent in high-speed videos. From a mechanical perspective, the flexural stiffness of the feather's shaft varies approximately as radius to the fourth power (Wainwright *et al.* 1976). This means a very slight decrease in the radius of the feather's shaft is potentially responsible for the bending of P8. The significance of such subtle variation in morphology may be easily overlooked.

The function of the sound is unknown. It is only produced by adult males, suggesting it has arisen via sexual selection. It appears to have most of the elements of a sonation (Bostwick & Prum 2003), except that it is apparently an inevitable product of flight, and thus may not be 'intentionally modulated'. Some of the males failed to produce sounds after being handled but could produce sound again after preening, suggesting that sound production could be modulated mechanically by disconnecting the barbs of the tips of P8 or P9. Moreover, males might also modulate the sound's production by varying the wingtip velocity via changes in wingbeat kinematics, such as during a mating display. It could thereby serve as an acoustic indicator of the male's flight capabilities.

All experiments were approved by the UC Berkeley Animal Care and Use Committee, and under permits issued by the National Environmental Protection Agency (NEPA) of Jamaica.

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