RESEARCH ARTICLE

Smithornis broadbills produce loud wing song by aeroelastic flutter of medial primary wing feathers

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ABSTRACT

Broadbills in the genus *Smithornis* produce a loud *brreeeeet* during a distinctive flight display. It has been posited that this klaxon-like sound is generated non-vocally with the outer wing feathers (P9, P10), but no scientific studies have previously addressed this hypothesis. Although most birds that make non-vocal communication sounds have feathers with a shape distinctively modified for sound production, *Smithornis* broadbills do not. We investigated whether this song is produced vocally or with the wings in rufous-sided broadbill (*S. rufolateralis*) and African broadbill (*S. capensis*). In support of the wing song hypothesis, synchronized high-speed video and sound recordings of displays demonstrated that sound pulses were produced during the downstroke, subtle gaps sometimes appeared between the outer primary feathers P6–P10, and wingtip speed reached 16 m s^{-1}. Tests of a spread wing in a wind tunnel demonstrated that at a specific orientation, P6 and P7 flutter and produce sound. Wind tunnel tests on individual feathers P5–P10 from a male of each species revealed that while all of these feathers can produce sound via aeroelastic flutter, P6 and P7 produce the loudest sounds, which are similar in frequency to the wing song, at airspeeds achievable by the wing tip during display flight. Consistent with the wind tunnel experiments, field manipulations of P6, P7 and P8 changed the timbre of the wing song, and reduced its tonality, demonstrating that P6 and P7 are together the sound source, and not P9 or P10. The resultant wing song appears to have functionally replaced vocal song.

KEY WORDS: Display, Sonation, Wind tunnel, Non-vocal communication, Locomotion-induced sound

INTRODUCTION

Of the many bird lineages that have evolved non-vocal acoustic signals produced with the wings or tail (Bostwick, 2006; Bostwick and Prum, 2003; Clark and Prum, 2015; Darwin, 1871; Manson-Bahr and Pye, 1985; Prum, 1998), hummingbirds, snipe and manakins are the only ones in which the physical mechanisms that produce these sounds have been investigated (Bahr, 1907; Bostwick and Prum, 2003, 2005; Clark and Feo, 2008; Hunter and Picman, 2005; Reddig, 1978). In other species thought to produce mechanical sounds, ornithologists have used three criteria, often implicitly, to identify their non-vocal origin: (1) a correlation between sound and motion, (2) proposed non-vocal quality to the

sound and (3) modified wing/tail feather morphology. While all three of these criteria are valuable, none is definitive. For instance, in contradiction with criterion 2, non-vocal and vocal sounds may sound alike (Bostwick and Zyskowski, 2001; Clark and Feo, 2010). Criterion 3 can be ambiguous, as most taxa that produce non-vocal sounds during ordinary flight lack obvious feather modifications (Clark and Prum, 2015).

Regarding criterion 1, everyday experience makes intuitive the correlation between sound and motion: footfalls produce footsteps, while vocalizations are accompanied by movement of the mouth. The correlation arises because sound is the result of motion. Though motions associated with vocalizations may be difficult to observe, hidden inside the animal, sounds produced by an animal's integument are produced by discrete, visible behaviors. Therefore, the observation of sound produced only in coordination with specific motions (e.g. during display) suggests the sound may be non-vocal. This is why taxa such as *Phoenicercus* cotingas (Snow, 1982; Trail and Donahue, 1991) or *Cnipodectes* flycatchers (Lane et al., 2007) are thought to produce mechanical sounds with their wings. But this criterion is not definitive because not all correlations are causal: an animal might vocalize in coordination with a particular flight display.

A clade with a distinctive flight display and associated sound are broadbills in the genus *Smithornis*, comprising African broadbill (*S. capensis*), rufous-sided broadbill (*S. rufolateralis*) and grey-headed broadbill (*S. sharpei*). Males produce sound during a stereotyped display by abruptly flying in a tight circle, landing where they began (Chapin, 1953). Accompanying the display is a loud, distinctive trilled *brreeeeet*. This striking sound is audible for over 100 m in dense forest, and sounds similar to a reedy, pulsatile klaxon horn. Hereafter, we term this sound 'song'. Of the various conflicting definitions of the term song widespread in the literature, we employ the functional definition: songs are sounds produced primarily (or exclusively) by males on their breeding territories and broadcast into the environment in an undirected fashion (even if also produced in a directed fashion, such as in response to playback). Our definition of song is not intended to imply homology with the socially learned vocal songs of the songbirds (oscine passerines) (Zeigler and Marler, 2008), because at the outset of our study on broadbills, how the sound was produced was unclear. As the song is produced only during this flight display, some have hypothesized that it is produced by the wings, i.e. wing song (Chapin, 1953; Fry, 1992; Lambert and Woodcock, 1996), while others have suggested it is vocal, i.e. vocal song (Bannerman, 1936; Lawson, 1961). Chapin (1953) described the outer wing feathers as stiff and slightly twisted (Fry, 1992; Wells, 2011), but did not identify the exact feathers that had these modifications.

Aeroelastic flutter is the mechanism that produces similar sounds in hummingbirds and snipe (Clark et al., 2011; Reddig, 1978). Flutter occurs when airflow over a stiff, thin object such as a feather causes it to oscillate at one or more stable frequencies (Alben and

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1069

Shelley, 2008; Bisplinghoff et al., 1996; Clark et al., 2013a,b, 2011). Research on hummingbird feathers has shown that flutter of an individual feather has several properties. Flutter only occurs above a critical airspeed (U^*). The frequency and mode of flutter (*sensu* Clark et al., 2013a) are determined by several independent variables, including feather morphology (size, shape, stiffness) and geometry (e.g. orientation relative to airflow, deformation). Interactions among neighboring feathers may also be important (Clark, 2011; Clark et al., 2011); in some species, a single feather is the sole source of sound, but in others, multiple feathers produce the sound in aggregate (Clark, 2014).

Here, we investigated the physical mechanism by which *Smithornis* species produce their distinctive songs. We first obtained synchronized high-speed videos and sound recordings of displays in the field. We then tested whether feathers and a whole wing may produce sound via a specific physical mechanism, aeroelastic flutter. Based on our wind tunnel results, we performed subsequent feather manipulation experiments in the field.

MATERIALS AND METHODS

This project was conducted under permits from the Tanzania Wildlife Research Institute (TAWIRI), the Tanzania Commission for Science and Technology (COSTECH) and Tanzania National Parks (TANAPA) to L.H. and A.N.G.K., and the Uganda Wildlife Authority and Uganda National Council for Science and Technology (UNCST) to A.N.G.K. and R.P., and was approved by the Yale University animal care protocol no. 2008-10906.

We obtained high-speed video of displaying African broadbills, *Smithornis capensis* (Smith 1840), in Kibale National Park, Kabarole province, 1500 m elevation (N 0.4915, E 30.3664) and rufous-sided broadbills, *Smithornis rufolateralis* Gray 1864, in Semliki National Park, Bundibugyo province, 800 m elevation (N 0.7129, E 29.9952), Uganda (24–29 June 2011). We recorded displays that were natural and those that were in response to playback. High-speed videos were recorded with a monochrome high-speed camera (Miro EX4) at a resolution of 800×600 pixels, with an Ai-S Nikkor 400 mm f/2.8 ED-IF lens. One video used in analyses was recorded at 500 frames s^{-1}, the remainder were recorded at 1265 frames s^{-1}. Because of the light conditions, the aperture was set wide open and shutter speed matched the frame rate (788 µs).

Sounds were recorded with a microphone (Sennheiser MKH 20) in a parabola (Telinga Pro Universal), connected to the first channel of a 24-bit digital recorder (Sound Devices 702) sampled at 96 kHz. The high-speed video and sound recordings were synchronized with the camera's trigger, which was routed through an amplifier and into the second channel of the recorder. The synchronization included a correction for sound delay: we measured the distance from the microphone to the bird's perch to the nearest meter with laser rangefinder binoculars (Leica Geovid 8×56 HD). We used this distance, and the speed of 340 m s^{-1}, to estimate the time taken for sound to travel from the bird to the microphone, which we added as a temporal offset to the sound, relative to the video. The bird flew roughly half a meter from the perch during the display, and given our precision of 1 m and the speed of sound, our synchronization precision was roughly 3 ms, or ±4 frames at 1265 frames s^{-1}.

One male African broadbill was collected and deposited in the Yale Peabody Museum (YPM 143025). The left wing was separated from the bird and dried spread, with the outer wing feathers in an orientation similar to that observed in mid-downstroke (Fig. S1). An additional set of wing feathers consisting of P5, P6, P7, P8, P9 and P10 was removed from one adult male museum skin each of *S. rufolateralis* (YPM 100551) and *S. capensis* (YPM 99997)

(Fig. S1). Both individual feathers and the spread wing were tested in a wind tunnel to reproduce the wing song, using the recording equipment and experimental setup described in Clark et al. (2013b) except for some minor modifications, described below.

The spread wing was mounted in the tunnel by clamping it with a ringstand clamp, which was attached at 90 deg to a sting projecting down into the airstream. The sting could be rotated from outside the tunnel, with the air on, which resulted in changes of the sweep angle of the wing, while angle of attack could be adjusted at the clamp, with the air off. The wing was tested over a range of airspeeds (up to 17 m s^{-1}) and angles of attack. The primaries were preened as necessary between trials to restore the contiguity of the feather vanes. During flapping flight, the exact position of each individual wing feather varies, relative to the position of neighboring wing feathers. As the spread wing was dried, and thus relatively rigid, it presumably did not perfectly duplicate this time-dependent millimeter-scale geometry and orientation of the individual wing feathers. Rather, our purpose in testing it was to qualitatively explore a range of orientations/airspeeds to search for one in which the wing produced a sound resembling the song, thereby providing a starting point for experiments on individual feathers, as described next.

To measure sound production quantitatively, individual feathers P5–P10 were mounted so that they projected down into the working section of the tunnel, following the same protocol and with the same equipment as in Clark et al. (2013b). Orientation was varied by rotating feathers about their longitudinal axis (varying the angle of attack) from outside the tunnel, while monitoring frequency with a live spectrogram trace. Feathers were initially tested at a relatively high airspeed (17.2 m s^{-1}) over a series of orientations, to explore how many modes of flutter they exhibited and how easy these were to elicit. We then selected an orientation corresponding to a mode that incorporated the feather's tip, and produced sound most similar in frequency to that of the wing song. Without further changes to the feather's orientation, airspeed was varied (in increments of 0.8 m s^{-1}) to determine the U^* for flutter, and to measure how frequency varied with airspeed. The presence of flutter was straightforward to observe by eye; high-speed videos were collected to determine whether the feather's tip was involved in flutter.

Informed by our wind tunnel results, we experimentally tested the role of wing feathers P6, P7 and P8 on three male African broadbills during the period June–September 2013 in Tanzania. We recorded display sounds of individuals before and after experimentally manipulating one or two feathers on each wing. Individual birds were mist netted in response to playback, and given a colored leg ring for identification after manipulation. At Zaraninge Forest in Saadani National Park, Coast region, 300 m elevation (S 6.13533, E 38.60676), we removed P8 from both wings of a male; at Amani, in the East Usambara Mountains, Tanga region, 984 m elevation (S 5.10157, E 38.62664), we clipped 2 cm from the tip of P7, and later 2 cm from the tip of P6 of both wings of the same individual; at Kilola Valley, Isunkaviola, in Ruaha National Park, Mbeya region, 1746 m elevation (S 7.70739, E 34.03046), we clipped 2 cm from the tip of P6 on both wings. All birds were released following feather manipulation after ensuring they were not stressed from the procedure. Recordings were obtained using a microphone (as above) connected to a Marantz PMD 661 digital recorder (16-bit, 48 kHz). Recordings of bird sonations following feather manipulation were obtained at least a day after manipulation.

Because the song is highly tonal, we tested for the effects of our manipulations by measuring entropy, also known as spectral flatness, a measure of the degree of tonality of sound (Tchernichovski et al., 2001; Thompson and Johnson, 2007) on recordings of individuals

before and after manipulation, using Raven Pro 1.4 software. More tonal sounds, with narrow peaks on power spectra, have low entropy, whereas spectrally flat sounds have high entropy; white noise has an entropy of 1. The 'average entropy' measurement in Raven provides a mean value for entropy for the entire frequency bandwidth and duration selected. We measured average entropy within the frequency bandwidth that encompassed the first three harmonics; higher harmonics were typically masked by background noise. The fundamental frequency of songs was measured from selection spectra. We calculated pulse rates (wingbeat frequency) from spectrograms, but excluded the first two pulses, which were typically performed at a slower and more variable rate, as well as the last one, which was of indeterminate length, but including the last inter-note interval, thus avoiding biases based on trill duration (Kirschel et al., 2009b, 2011). We tested whether feather manipulation affected the entropy of the sound produced using multiple linear regression (STATA 11, StataCorp) including average entropy of background noise as a fixed factor, to control for variation in average entropy that could result from differences in background noise, such as produced by insects (Kirschel et al., 2009a). Average entropy of background noise was measured from 1 s of recording just before or after each song. Normality of residuals was verified using the skewness–kurtosis test.

RESULTS
Field observations and video analyses
Individual male broadbills displayed spontaneously on perches within their territories, and they responded vigorously to playback,

approaching and increasing the frequency of display. We did not observe female broadbills displaying in response to playback, but females did occasionally approach in response to playback, suggesting the song could function in mate attraction. These observations accord with the view that *Smithornis* displays and accompanying wing song serve similar functions to vocal song in other passerines, based on the aggressive responses to playback of display sounds by males presumably in search of an intruder. Territorial birds often also vocalized prior to displays (Fig. S2). These were typically tonal frequency sweeps audible only at short distances, and likely function in short-distance communication.

Males displayed from perches ranging from 2 to 15 m above ground. The display kinematics were similar in each species (see Movies 2 and 3). First, a male flew to a branch and perched quietly. Then, over the course of about 1 s, he flew in a tight circle approximately 0.5 m in diameter (Fig. 1A). The plane of this circle varied from horizontal to nearly vertical. The male typically leapt 10–30 cm above the perch, then commenced flapping and followed a curving path before returning to the same perch (Fig. 1A), landing within 20 cm of the take-off position. He perched on average for 20 s before repeating the display. Males sometimes performed over a dozen displays from a single perch before moving to another.

We recorded high-speed videos synchronized with sounds of 34 displays, including a combination of backlit shots from below the bird and videos level with the bird against a dark background (see Movie 2). Of these, we quantitatively analyzed nine high-quality videos from two male African broadbills (distance from birds:
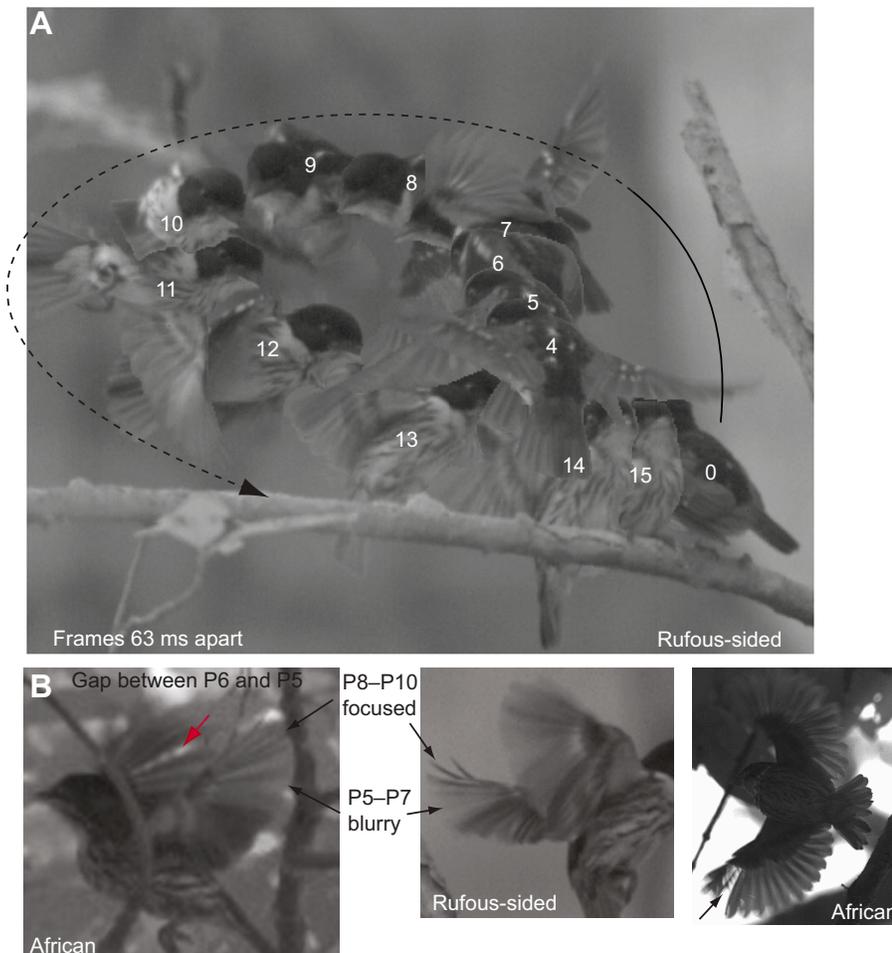

Fig. 1. Kinematics of rufous-sided (*Smithornis rufolateralis*) and African broadbill (*S. capensis*) displays. See also Movies 2 and 3. (A) Thirteen frames (out of 1230) of the display, from a high-speed video. Starting from a perch, the male jumped and yawed 180 deg (before frame 0, not shown), then flew in a tight circle and landed on the perch (frames 0–15). Each frame is 0.063 s apart; frames 1–3 have been omitted for clarity. (B) Frames from mid-downstroke, demonstrating greater blurriness of P5–P7 than P8–P10, and gaps that occasionally appear between primaries.
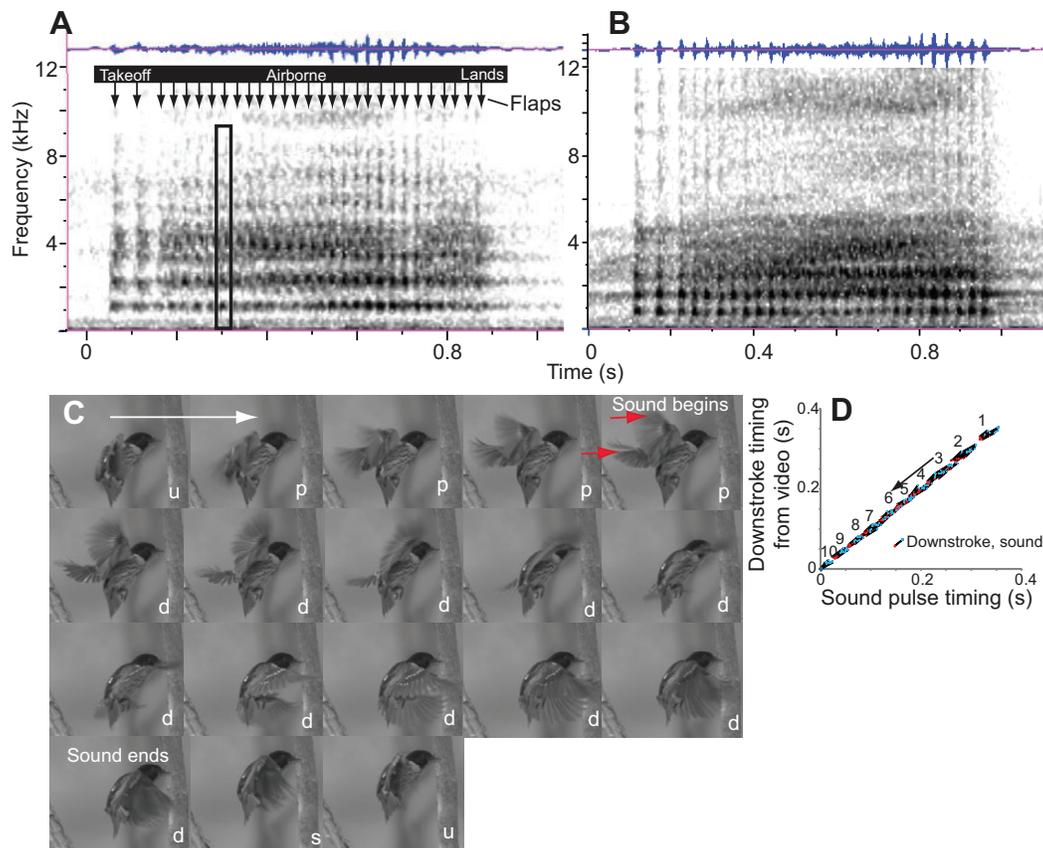
Fig. 2. Wing song of rufous-sided and African broadbills showing correspondence between sound and motion. The song was a series of pulses of sound with a fundamental frequency of 1.1 kHz in rufous-sided broadbill (A) and 0.8 kHz in African broadbill (B), plus harmonics. Black arrows in A indicate 29 pulses of sound and wing flaps. The boxed region corresponds to the wingbeat shown in C. Hann fast Fourier transform (FFT), 50% overlap, 1024-sample window (96 kHz sampling frequency). (C) A single wingbeat from video synchronized with the sound recording shown A. Frames are 1.58 ms apart. u, upstroke; p, pronation; d, downstroke; s, supination. Red arrows indicate gaps that appear between outer primaries during pronation. (D) Relative timing of 10 consecutive downstrokes, from high-speed video and sound pulses, from nine displays of African broadbill and six displays of rufous-sided broadbill. Sound pulses and downstrokes coincide almost exactly (slope=1.001, r^2=0.998 averaged across all data). Numbers correspond to wingbeats, where trials are aligned relative to the end of the 10th downstroke.

15–31 m) and six from one male rufous-sided broadbill (distance: 13 m).

A male usually initiated the display by jumping and rotating 180 deg in yaw. This maneuver allowed the bird to turn around so that he would then land facing the original direction. Sometimes, after yawing he then landed, paused momentarily, then leapt a second time to continue the display. He then flapped his wings continuously as he flew the course of the circuit, returning to the perch (Fig. 1A). The introductory 1–3 wingbeats were distinct, with a slightly lower frequency and slightly higher stroke amplitude than the rest. Through the remaining display, the wingbeat frequency was 28.6±1.3 Hz (African broadbill, N=2) and 32.4 Hz (rufous-sided broadbill, N=1). For comparison, in takeoff for ordinary flight, an African broadbill had a wingbeat frequency of 25.4 Hz (N=1; from high-speed video).

The high-speed videos provide a rough estimate of the wing feather velocity during the downstroke. Each downstroke lasted roughly 0.02 s (Fig. 2C), and the wing length was 0.1 m. Assuming the wing was held straight and was flapped sinusoidally with a stroke amplitude of 180 deg, the wingtip would reach 16 m s^{-1} during the downstroke. This represents an upper bound, because the actual stroke amplitude appeared to be somewhat less than 180 deg, wing length during flapping flight is unknown, and the wing was unlikely to have been held straight.

There was a 1:1 correspondence between sound pulses and wing beats in the display (Fig. 2; N=15 synchronized videos and sounds). In particular, each pulse of sound was produced for the duration of the downstroke (Fig. 2C). Our estimate of the exact onset of the sound varied from 5 to −5 ms relative to the end of wing pronation (i.e. rotation of the wing into position for the downstroke), and sound cessation varied from 5 to −4 ms relative to the beginning of supination (i.e. rotation of the wing at the end of the downstroke; Fig. 2C). Our error was thus roughly 10% of the wingbeat duration, which lasted ~50 ms (Fig. 2C). Fundamental frequency varied little over the display (Fig. 2). The timbre and energy content of individual trill pulses varied through the course of the maneuver, with the loudest sound produced mid-turn as the bird began returning to the perch.

Because of limited light in the forest understory, we were restricted to a shutter speed of 788 μs, resulting in blurry wingtips mid-downstroke (Fig. 1B). The mechanism of sound production was therefore not immediately obvious from high-speed video. However, frame-by-frame examination of the videos yielded several consistent observations about downstroke kinematics that provide clues about mechanism. There was clear bending and separation of the tips of P10, P9 and P8 during downstroke (red arrows in Figs 1B, 2C), which was slightly more pronounced than in a video of ordinary flight. Separation of the outermost primaries began early in wing pronation, slightly before our estimated onset of sound
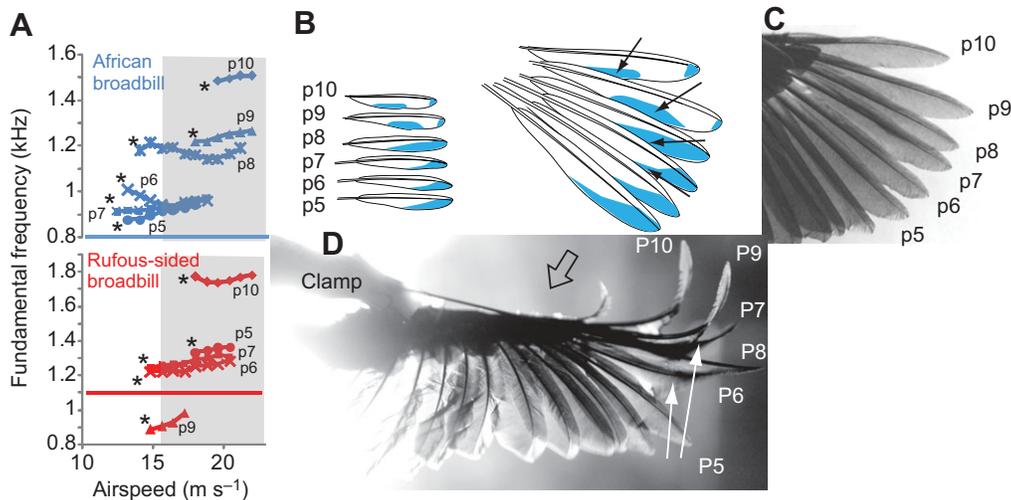
Fig. 3. Results of wind tunnel experiments to elicit flutter and sound from *Smithornis* wing feathers. (A) Fundamental frequency of sound generated by aeroelastic flutter of individual primary feathers P5–P10 in a wind tunnel. Gray area indicates airspeeds that exceed the estimated maximum wingtip velocity of 16 m s^{-1}, making them biologically unrealistic. Asterisk indicates U^*, the lowest airspeed at which the feather made sound (see also Table S1; Clark and Prum, 2015). Horizontal blue and red lines indicate the fundamental frequency of song produced by the bird (see Fig. 3). P7, P6 and, in African broadbill, P5 generated sounds most similar to the song frequency. P8 from rufous-sided broadbill showed similar patterns to African broadbill P8, but is not depicted as it was lost prior to quantitative data collection. (B) Left: feather region that fluttered, when feathers were tested individually in the wind tunnel (blue). Right: feathers in the approximate orientation of a spread wing, showing regions of overlap (arrows) that likely prevent flutter. (C) Wing of a male African broadbill (YPM 143025). (D) African broadbill wing (YPM 143025) producing sound in the wind tunnel, at an airspeed of 17 m s^{-1} (open arrow indicates approximate direction of airflow). The outer primaries bent and twisted (particularly P10, P9 and P7) and gaps appeared around P7 and P6. These feathers fluttered (white arrows) at about 0.9 kHz. See Movie 1 for a high-speed video of wing fluttering in the wind tunnel.

production (Fig. 2C). P7 and P6 also appeared to bend significantly, with light appearing between primaries proximal to P8 in some video frames. This was not an artifact caused by overexposure. Primaries P6 and P7 were always blurry, and sometimes blurrier than P9 and P10 (Fig. 1B). Physical contact only rarely occurred, and then only between the wings at the end of the downstroke of the first two flaps, indicating the acoustic mechanism is not percussive (Bostwick and Prum, 2003).

Wind tunnel results

The African broadbill spread wing was tested at airspeeds between 15.8 and 17.2 m s^{-1}. At these speeds, the tips of the outer primaries bent to a similar degree to that observed during the display (Fig. 3D; Movie 1). A large gap always appeared between P10 and P9, but neither of these feathers fluttered or produced sound at any orientations and airspeeds tested. At certain orientations and airspeeds, smaller gaps appeared on either side of P8, as well as a gap between P7 and P6. When this occurred, P7 and especially P6 fluttered and produced a tonal sound with a fundamental frequency of 0.94 kHz. The relative power of higher harmonics compared with the fundamental frequency was lower than that recorded in display song (Fig. 2; Fig. S3).

In tests of individual feathers, it was relatively difficult to find orientations that repeatably elicited flutter from P10, P9 and P8. By contrast, flutter was easily elicited from P7, P6 and P5. P7 and P6 produced frequencies and U^* values most consistent with wing song (Fig. 3A), while P9, P10 and P5 (P5 in rufous-sided broadbill only) produced U^* values higher than the estimated wingtip velocity (gray region in Fig. 3A). The frequencies of P9 and P10 were less similar to wing song frequencies than those produced by P7 and P6.

Feather manipulation experiments

Manipulation of wing feathers of three male African broadbills provided further evidence for the role of certain primary feathers in

sound production. All three males produced typical sounds prior to manipulation. Each manipulation significantly reduced the tonality (increased average entropy) of the sound produced relative to sound recordings of the same male before manipulation: (1) P8 removed (Zaraninge; N=30, t=12.04, r^2=0.84, P<0.001; Fig. S4); (2) 2 cm of tip of P7 clipped (Amani; N=18, t=12.00, r^2=0.90, P<0.001), then 2 cm of P6 clipped on the same bird (N=49, t=13.65, r^2=0.80, P<0.001; Fig. 4; Fig. S5); and (3) 2 cm of P6 clipped (Isunkaviola; N=31, t=3.81, r^2=0.47, P=0.001; Fig. S4) – example sound recordings before and after experimental manipulation are provided in Audio 1–7. Average entropy of background noise did
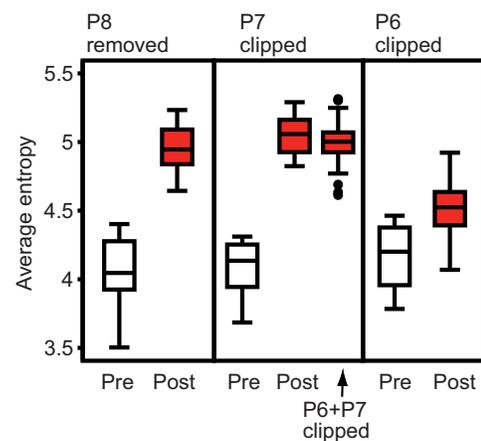

Fig. 4. Average entropy of African broadbill sounds produced by three individuals before and after feather manipulation (shaded boxplots) from three populations in Tanzania. Entropy increased significantly when P8 was removed, when P6 or P7 were clipped, and when both were clipped. Line shows median, boxes represent the interquartile range (IQR) and whiskers ±1.5 IQR.

not differ before and after manipulation for any experiment (all $P>0.05$). All results shown were from models with the lowest Akaike information criterion (AIC) scores.

DISCUSSION

Smithornis broadbills produce a startlingly loud sound via aeroelastic flutter of their primary wing feathers. The sound source appears to be centered on P6 and P7. This conclusion is supported by three independent lines of evidence: high-speed video of displays (Figs 1 and 2), wind tunnel tests that reproduce the mechanism (Fig. 3), and experimental manipulation of wild birds to demonstrate the necessity of P6, P7 and P8 for production of normal song (Fig. 4). Our results also imply that more than one feather produces the wing song, as none of our manipulations eliminated sound production entirely. This remarkable sound is audible at long distances through the forest understory, and can be considered song as it appears to have the same function as vocal song in other birds.

Mechanism

Our data indicate that *Smithornis* broadbills produce their wing song via aeroelastic flutter, the same physical mechanism underlying a range of sounds in hummingbirds (Clark et al., 2013a,b, 2011) and snipe (Reddig, 1978). Wind tunnel data demonstrate the physical sufficiency of fluttering feathers to produce sound at the correct frequency and airspeed, and in feather regions that do not overlap neighboring feathers in a spread wing (Fig. 3). Our data imply there is no single feather crucial for sound production (Clark, 2014), and, instead, multiple wing feathers contribute to produce sound. Both lab and field data implicate P6 and P7 in sound production, and while our data do not resolve the exact role of P5 and P8, P9 and P10 do not appear to contribute to sound production.

In the wind tunnel, feathers P6 and P7, and, to a lesser degree, P8 and P5, had U^* for flutter that fell below estimated wingtip speed (Fig. 3A), meaning that they flutter at airspeeds likely reached by the wing. Moreover, isolated P9 and P10 fluttered in regions where the feathers would likely overlap with one another in the spread wing, precluding flutter (Fig. 3B–D). Although the frequency of flutter of P6 and P7 was most similar to wing song, it was above the song frequency in each species (Fig. 3A), and harmonics produced by isolated feathers were weaker than they are in the wing song (Fig. S3). Two reasons may explain these minor discrepancies. First, properties of feather flutter can be influenced by adjacent feathers (Clark et al., 2011). These effects are not replicated in our wind tunnel experiments on single feathers. Second, wing song is produced by a flapping wing that is accelerating and decelerating, whereas the wind tunnel experiments matched fluid velocity but not acceleration. How acceleration may affect the initiation of flutter, and U^*, remains unclear.

The field manipulations indicated that the distal 2 cm of P6 and P7 are necessary for tonal sound production in *S. capensis*. They also imply that P8 plays a role, as each of these manipulations resulted in increased entropy in wing song relative to sounds produced before manipulation (Fig. 4; Figs S4, S5). The increased entropy indicated that the manipulations disrupted the limit-cycle oscillatory mechanism at the sources of the sound, increasing chaotic (atonal) components of motion of the source. However, as none of our manipulations entirely eliminated the song, but rather transformed it from a tonal sound reminiscent of the sound produced by a klaxon to one that was less tonal, sounding more like a ratchet, our result also implies that none of these feathers is a linchpin for sound production (*sensu* Clark, 2014) and that sound is also produced by some additional region of the wing unaffected by our

manipulations. The likeliest regions that contribute to sound production are portions of P6 and P7 proximal to the tip that we removed, and/or P5. Under a source-filter model of how feathers produce sound (Clark, 2014), we hypothesize P6 and P7 are co-sources, with P5 and P8 as filters. Alternatively, P8 and/or P5 might also be sources, but this is not entirely supported by our wind tunnel experiments (Fig. 3).

Evolution of mechanical sounds

The production of the wing song of *Smithornis* can be considered a 'cryptic' mechanism of sound production, because the wing feathers that produce the sound do not have any clear or obvious morphological modifications for sound production (Fig. 3C). We suggest that, unlike most birds that produce mechanical sounds, any morphological variation associated with mechanical sound production by *Smithornis* feathers is not visible to the naked eye. This is not to imply that there are no such modifications; we expect these feathers do have microscopic morphological modifications that tune how they flutter and produce sound, for instance by affecting vane stiffness. These modifications are difficult to identify from gross morphology (Fig. 3; Fig. S1), or to distinguish from the diversity of shapes of outer wing feathers that are driven by other aerodynamic functions. While the individual feathers of *Smithornis* wings do differ slightly in shape and stiffness (Fig. S1), all feathers across all bird wings vary in size and shape. Which subtle shape changes may relate to sound production and which do not is unclear.

Our result shows that morphological adaptations for feather sound production might not be revealed from casual morphological observations of morphology, e.g. a bird in the hand or a museum skin. Rather, of the three criteria often used to diagnose non-vocal sound production, the strongest evidence is observation of a correlation between kinematics (such as of a display) and sound production. Our result implies that there may be other bird taxa with poorly known natural history and unremarkable feathers, which produce distinctive non-vocal sounds. In conclusion, though distinctively shaped feathers, when present, provide a strong clue as to whether and how a bird produces a sonation, the reverse is not true: mechanical sounds may be produced by feathers that do not have a notable or distinctive shape (Clark, 2008). This is congruent with our finding that essentially any pennaceous feather can be induced to flutter and generate sound in a wind tunnel (Clark et al., 2013a,b; Clark and Prum, 2015), i.e. flutter of any flight feather may arise as a passive byproduct of locomotion.

It is not yet known whether evolution of this unique mechanism of sound production in *Smithornis* was driven more by male–male competition or female choice. *Smithornis* wing song was at times broadcast into the environment like the vocal advertisement song of songbirds. In addition to serving a territorial function, the display is performed before copulation (Chapin, 1953). Though visually impressive, the display did not seem particularly taxing. A single display lasts only 1 s and therefore consumes negligible energy (Barske et al., 2014; Clark, 2012). Males performed hundreds of flights over the course of the day, and did not seem to tire when responding to playback. During sonations produced by manakins (Bostwick and Prum, 2003), some hummingbirds (Feo and Clark, 2010) and flappet larks (Norberg, 1991), males increase wingbeat frequency to as much as double that of ordinary flight, resulting in displays that appear physically demanding (Barske et al., 2014). By contrast, male broadbills only slightly increased wingbeat frequency (12%) over wingbeat frequency of ordinary flight, suggesting little physical demand. Wing song may reveal the condition of male plumage: we observed one male to naturally produce high entropy

sound and, upon capture, we found he had very worn wing feathers (A.N.G.K., personal observation). But, overall, the evidence does not strongly support an adaptive explanation of the evolved replacement of vocal song with a display that better conveys information about male quality. We suggest that, instead, this sonation has evolved as an arbitrary replacement for vocal song through a Fisherian or Lande–Kirkpatrick sexual selection process (Prum, 2010).

References
Alben, S. and Shelley, M. J. (2008). Flapping states of a flag in an inviscid fluid: bistability and the transition to chaos. *Phys. Rev. Lett.* **100**, 074301.
Bahr, P. H. (1907). On the "Bleating" or "Drumming" of the Snipe (*Gallinago coelestis*). *Proc. Zoolog. Soc. Lond.* **77**, 12-35.
Bannerman, D. A. (1936). *Birds of Tropical West Africa*. London: Crown Agents.
Barske, J., Fusani, L., Wikelski, M., Feng, N. Y., Santos, M. and Schlinger, B. A. (2014). Energetics of the acrobatic courtship in male Golden-collared Manakins (*Manacus vitellinus*). *Proc. R. Soc. B Biol. Sci.* **281**, 20132482.
Bisplinghoff, R. L., Ashley, H. and Halfman, R. L. (1996). *Aeroelasticity*. Mineola, New York: Dover Publications, Inc.
Bostwick, K. S. (2006). Mechanisms of feather sonation in Aves: unanticipated levels of diversity. *Acta Zoolog. Sin.* **52S**, 68-71.
Bostwick, K. S. and Prum, R. O. (2003). High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *J. Exp. Biol.* **206**, 3693-3706.
Bostwick, K. S. and Prum, R. O. (2005). Courting bird sings with stridulating wing feathers. *Science* **309**, 736.
Bostwick, K. and Zyskowski, K. (2001). Mechanical sounds and sexual dimorphism in the Crested Doradito. *Condor* **103**, 861-865.
Chapin, J. P. (1953). The birds of the Belgian Congo. Part 3. *Bull. Am. Coll. Museum Nat. His.* **75**, 4-820.
Clark, C. J. (2008). Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. *Biol. Lett.* **4**, 341-344.
Clark, C. J. (2011). Wing, tail, and vocal contributions to the complex signals of a courting Calliope Hummingbird. *Curr. Zool.* **57**, 187-196.
Clark, C. J. (2012). The role of power versus energy in courtship: what is the 'energetic cost' of a courtship display? *Anim. Behav.* **84**, 269-277.
Clark, C. J. (2014). Harmonic hopping, and both punctuated and gradual evolution of acoustic characters in Selasphorus hummingbird tail feathers. *PLoS ONE* **9**, e93829.

Clark, C. J. and Feo, T. J. (2008). The Anna's Hummingbird chirps with its tail: a new mechanism of sonation in birds. *Proc. R. Soc. B Biol. Sci.* **275**, 955-962.
Clark, C. J. and Feo, T. J. (2010). Why do *Calypte* hummingbirds "sing" with both their tail and their syrinx? An apparent example of sexual sensory bias. *Am. Nat.* **175**, 27-37.
Clark, C. J. and Prum, R. O. (2015). Aeroelastic flutter of feathers, flight and the evolution of non-vocal communication in birds. *J. Exp. Biol.* **218**, 3520-3527.
Clark, C. J., Elias, D. O. and Prum, R. O. (2011). Aeroelastic flutter produces hummingbird feather songs. *Science* **333**, 1430-1433.
Clark, C. J., Elias, D. O., Girard, M. B. and Prum, R. O. (2013a). Structural resonance and mode of flutter of hummingbird tail feathers. *J. Exp. Biol.* **216**, 3404-3413.
Clark, C. J., Elias, D. O. and Prum, R. O. (2013b). Hummingbird feather sounds are produced by aeroelastic flutter, not vortex-induced vibration. *J. Exp. Biol.* **216**, 3395-3403.
Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. Princeton, NJ: Princeton University Press.
Feo, T. J. and Clark, C. J. (2010). The displays and sonations of the Black-chinned Hummingbird (Trochilidae: *Archilochus alexandri*). *Auk* **127**, 787-796.
Fry, C. H. (1992). Eurylaimidae, broadbills. In *The Birds of Africa*, Vol. 4 (ed. S. Keith, E. K. Urban and C. H. Fry). New York: San Diego.
Hunter, T. A. and Picman, J. (2005). Characteristics of the wing sounds of four hummingbird species that breed in Canada. *Condor* **107**, 570-582.
Kirschel, A. N. G., Blumstein, D. T., Cohen, R. E., Buermann, W., Smith, T. B. and Slabbekoorn, H. (2009a). Birdsong tuned to the environment: green hylia song varies with elevation, tree cover, and noise. *Behav. Ecol.* **20**, 1089-1095.
Kirschel, A. N. G., Blumstein, D. T. and Smith, T. B. (2009b). Character displacement of song and morphology in African tinkerbirds. *Proc. Natl. Acad. Sci. USA* **106**, 8256-8261.
Kirschel, A. N. G., Cody, M. L., Harlow, Z. T., Promponas, V. J., Vallejo, E. E. and Taylor, C. E. (2011). Territorial dynamics of Mexican Ant-thrushes Formicarius moniliger revealed by individual recognition of their songs. *Ibis* **153**, 255-268.
Lambert, F. R. and Woodcock, M. (1996). *Pittas, Broadbills and Asities*. East Sussex: Pica Press.
Lane, D. F., Servat, G. P., Valqui, H. T. and Lambert, F. R. (2007). A distinctive new species of tyrant flycatcher (passeriformes: tyrannidae: *Cnipodectes*) from southeastern Peru. *Auk* **124**, 762-772.
Lawson, W. J. (1961). Probable courtship behaviour of the broadbill *Smithornis capensis*. *Ibis* **103a**, 289-290.
Manson-Bahr, P. H. and Pye, J. D. (1985). Mechanical Sounds. In *A Dictionary of Birds* (ed. B. Campbell and E. Lack), pp. 342-344. Vermillion, SD: Buteo Books.
Norberg, R. Å. (1991). The flappet lark *Mirafra rufocinnamomea* doubles its wingbeat rate to 24hz in wing-clap flight display: a sexually selected feat. *J. Exp. Biol.* **159**, 515-523.
Prum, R. O. (1998). Sexual selection and the evolution of mechanical sound production in manakins (Aves: pipridae). *Anim. Behav.* **55**, 977-994.
Prum, R. O. (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.
Reddig, E. (1978). Der ausdrucksflug der Bekassine (*Capella gallinago gallinago*). *J. Ornithol.* **119**, 357-387.
Snow, D. W. (1982). *The Cotingas*. London: British Museum.
Tchernichovski, O., Mitra, P. P., Lints, T. and Nottebohm, F. (2001). Dynamics of the vocal imitation process: How a zebra finch learns its song. *Science* **291**, 2564-2569.
Thompson, J. A. and Johnson, F. (2007). HVC microlesions do not destabilize the vocal patterns of adult male zebra finches with prior ablation of LMAN. *Dev. Neurobiol.* **67**, 205-218.
Trail, P. W. and Donahue, P. (1991). Notes on the behavior and evology of the red-cotingas (Cotingidae: *Phoenicircus*). *Wilson Bull.* **103**, 539-551.
Wells, D. R. (2011). Unique mid-tract loss of a primary remex in male broadbills of the Southeast Asian genus *Calyptomena*: timing and possible implications. *Ibis* **153**, 429-432.
Zeigler, H. P. and Marler, P. (2008). *Neuroscience of Birdsong*. Cambridge: Cambridge University Press.