

RESEARCH ARTICLE

Aeroelastic flutter of feathers, flight and the evolution of non-vocal communication in birds

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ABSTRACT

Tonal, non-vocal sounds are widespread in both ordinary bird flight and communication displays. We hypothesized these sounds are attributable to an aerodynamic mechanism intrinsic to flight feathers: aeroelastic flutter. Individual wing and tail feathers from 35 taxa (from 13 families) that produce tonal flight sounds were tested in a wind tunnel. In the wind tunnel, all of these feathers could flutter and generate tonal sound, suggesting that the capacity to flutter is intrinsic to flight feathers. This result implies that the aerodynamic mechanism of aeroelastic flutter is potentially widespread in flight of birds. However, the sounds these feathers produced in the wind tunnel replicated the actual flight sounds of only 15 of the 35 taxa. Of the 20 negative results, we hypothesize that 10 are false negatives, as the acoustic form of the flight sound suggests flutter is a likely acoustic mechanism. For the 10 other taxa, we propose our negative wind tunnel results are correct, and these species do not make sounds via flutter. These sounds appear to constitute one or more mechanism(s) we call ‘wing whirring’, the physical acoustics of which remain unknown. Our results document that the production of non-vocal communication sounds by aeroelastic flutter of flight feathers is widespread in birds. Across all birds, most evolutionary origins of wing- and tail-generated communication sounds are attributable to three mechanisms: flutter, percussion and wing whirring. Other mechanisms of sound production, such as turbulence-induced whooshes, have evolved into communication sounds only rarely, despite their intrinsic ubiquity in ordinary flight.

KEY WORDS: Locomotion, Pennaceous feather, Sonation, Sound, Wing whirring

INTRODUCTION

Darwin (1871) observed that birds such as snipe, hummingbirds or manakins make extensive use of non-vocal ‘instrumental music’ during courtship. To explain how such sounds arise, he suggested: ‘...birds during their courtship flutter, shake, or rattle their unmodified feathers together; and if the females were led to select the best performers, the males which possessed the strongest or thickest, or most attenuated feathers... would be the most successful’ (p. 67). In other words, incidental non-vocal sounds that accompany motions may become salient to receivers and evolve into communication signals (Bostwick and Prum, 2003, 2005; Prum, 1998). For this to occur, first, a mechanism of sound production must be a passive byproduct of locomotion and, second,

the evolutionary modification of behavior or morphology (e.g. feather shape) must produce variation in acoustic qualities that may then be the target of selection for communication. Here, we focus on one mechanism by which feathers produce sound, aeroelastic flutter, previously demonstrated for hummingbirds (Clark et al., 2013a,b, 2011) and snipe (Reddig, 1978). We present data suggesting that aeroelastic flutter and the ensuing flutter-induced sounds satisfy both of the aforementioned requirements.

Ordinary flight produces locomotion-induced sounds by several poorly described mechanisms, which can be distinguished in part by their acoustic properties. Four such mechanism categories are as follows. (1) Whooshing sounds produced by turbulent airflow shed with each wingbeat (Blake, 1986; Sarradj et al., 2011). Whooshes tend to be quiet and atonal, with most acoustic energy <1 kHz (Sarradj et al., 2011), but they can be loud in fast flight, such as a falcon (*Falco* sp.) chasing prey at high speed (e.g. falcon chasing a dove in Audio 1; band-tailed pigeon flock in Audio 2). (2) Rustling sounds, which are atonal, complex, time varying, and contain sound energy at higher frequencies. Their physical acoustic mechanism is unclear, possibly slip and stick friction (Patek, 2001), because feathers slide over each other as the flight feathers flex and reposition during the wingbeat. Such sounds seem common in the flight of some birds, such as in gallinaceous birds. (3) Snaps and claps, which are percussive sounds caused by forced airflow and collisions between the wings and another body part (e.g. black-tailed trainbearer in Audio 3; booted racket-tail in Audio 4; and wire-crested thornail in Audio 5). They are short, broad frequency and impulsive (Bostwick and Prum, 2003). Claps regularly occur in ordinary flight, such as the clapping sounds rock doves (*Columba livia*) occasionally produce during takeoff. (4) Tonal flight sounds, which are generated during ordinary flight of birds such as hornbills and ducks (e.g. black-and-white-casqued hornbill in Audio 6; black vulture in Audio 7; and eared dove in Audio 8). This final category includes the sounds that are the focus of this study: tonality implies a stable, oscillatory source. It is out of passive mechanisms such as these that communication sounds may arise.

During aerial displays, some hummingbirds produce communication sounds by aeroelastic flutter of their wing and tail feathers (Clark et al., 2013a,b, 2011). Aeroelastic flutter (hereafter, flutter) results from dynamic coupling of aerodynamic forces with the geometry and stiffness of a wing or tail feather, to produce a limit cycle vibration (i.e. a stable oscillation) of a portion of a feather. In essence, at a particular orientation, when air velocity over the feather exceeds a threshold (U^*), a feather becomes an aerodynamically driven oscillator. Flutter of hummingbird feathers usually produces tonal sound with strong harmonics (Clark et al., 2013a,b, 2011; Clark and Feo, 2008, 2010). We hypothesized that the capacity to flutter is intrinsic to all pennaceous flight feathers in the right airflow. If so, congruent with Darwin’s (1871) hypothesis, flutter-induced acoustic signals may readily evolve out of initially involuntary, incidental byproducts of avian flight mechanics.

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To test this hypothesis, we gathered reports in the literature of sounds produced with the wings or tail, to assess the diversity of flight sounds. Then, we surveyed sound collections including the Macaulay Library, Xeno-Canto and the British Library of Wildlife Sounds for recordings of non-vocal avian sounds. We used acoustic characters in these sounds to develop hypotheses of their physical origin. To test the flutter hypothesis in particular, we measured the capacity of individual feathers to flutter and produce tonal sounds in a wind tunnel. Our sample included feathers with modified shapes hypothesized to have evolved to produce display sounds, such as tail feathers of an adult male lyre-tailed honeyguide (*Melichneutes robustus*; Friedmann, 1955), and feathers lacking any obvious modifications for sound production, from taxa that produce tonal sound during ordinary flight, such as ducks.

Previous results on hummingbird feathers suggested that all individual, isolated feathers can flutter under the right aerodynamic conditions (Clark et al., 2013b). Many of the inducible modes of flutter do not correspond to sounds produced by birds in flight and are thus spurious (Clark et al., 2013a). Therefore, the ability to flutter in a wind tunnel does not indicate that a feather actually flutters during natural behavior of the bird. We developed four criteria for whether a mode of flutter induced in the wind tunnel was a match to the flight sound. (1) The motion was a limit cycle oscillation (i.e. stable and periodic, not chaotic), with a frequency within 25% of the fundamental frequency, 2nd or 3rd harmonic of the flight sound, and with similar harmonic structure. (2) The airspeed necessary to induce flutter was low enough to be a plausible flight speed, or the speed of the wing tip during flapping flight (ignoring acceleration). (3) The portion of the feather that fluttered was likely to be free to flutter during flight (Clark et al., 2013a; Feo and Clark, 2010). The proximal portion of the trailing vane of most flight feathers is normally covered by neighboring feathers, so it is not free to flutter. Even if this portion of a feather vane readily flutters in the wind tunnel, this mode of flutter is unlikely to be produced in bird flight. (4) The mode of flutter was strong, loud and repeatably elicited at a feather orientation plausible for a flying bird. When tested at implausible orientations, such as with the trailing vane pointed upwind, all feathers will contort and express clearly spurious modes of flutter (Clark et al., 2013a).

MATERIALS AND METHODS

Wind tunnel experiments

We obtained feathers from taxa that produce tonal flight sounds, either in ordinary flight or in displays, to test in a wind tunnel. In taxa that had feathers apparently modified for sound production, the modified feather were sampled. In taxa apparently lacking modifications, outer primaries (P10 and P9) were sampled, because these tend to be emarginated, which we hypothesized made them prone to flutter. We obtained one or more outer wing feathers (primaries, P5–P10, in which P10 is the outermost wing feather) from 27 taxa from 12 families, and one or more outer tail feathers (rectrices, R3–R8) from seven species of snipe (*Gallinago* spp.) and lyre-tailed honeyguide. Feathers were taken from males only, and from live sources, alcohol-preserved specimens or dried museum skins. Feathers were plucked, or the shaft was cut near the calamus, when plucking might have resulted in damage to the specimen. All feathers sampled were in good condition, with little apparent damage from collection/preservation. Feathers were obtained from specimens from the Yale Peabody Museum (YPM); American Museum of Natural History (AMNH); Museum of Vertebrate Zoology (MVZ); Louisiana State University Museum of Zoology (LSUMZ); the Livingston Ripley Waterfowl Conservancy (www.lrwc.net); or from colleagues.

Individual feathers were mounted in a wind tunnel, perpendicular to flow, to test their aerodynamic and aeroacoustic response to airflow. The equipment and setup were the same as, and the protocol similar to, that described in Clark

et al. (2013b) and is repeated here briefly. The feathers were mounted by inserting an insect pin (small feathers) or dissecting pin (large feathers) into the calamus and anchored with a small amount of cyanoacrylate glue. The other end of this pin was then inserted into a pin vise, which projected vertically on a sting down into the freestream of the tunnel, with the feather's long axis perpendicular to flow, as in fig. 2 of Clark et al. (2013b). Because of the floor and ceiling boundary layers (Clark et al., 2013b), there was only approximately 20 cm of usable space within the working section. For feathers longer than 20 cm (from ducks and common raven), either the feather shaft was cut and only the distal portion was tested, or the sting was retracted into the roof of the tunnel so that the distal portion of the feather projected out of the boundary layer into the freestream. Orientation of the feather could be varied by bending the pin, or by rotating the sting.

To measure a feather, the wind tunnel was initially set to a speed slightly above the presumed flight speed of the bird from which it came (12 m s^{-1} for small passerines, up to 25 m s^{-1} for ducks). The feather's orientation was then adjusted to find modes of flutter, and airspeed was increased, as needed. If a mode of flutter was found that was similar to the flight sound of the bird from which the feather came, we then collected data at constant orientation, over a range of airspeeds, as in Clark et al. (2013b). If after testing 5–10 orientations/airspeeds, no matching mode of flutter was found, we returned to conditions that elicited the mode of flutter that produced the loudest sound and/or was the most stable over varying airspeeds, and obtained measurements over a range of speeds, at a constant orientation.

We recorded the feather's sounds with a microphone positioned close to the feather (often <10 cm), though not in the aerodynamic wake, with all of the same methodological caveats described in Clark et al. (2013a,b). High-speed videos were recorded at a subset of speeds to identify the feather region that fluttered.

To test whether alcohol preservation or specimen age may affect the material properties of feathers, we sampled two Anna's hummingbird outer rectrices (R5), one from a museum skin collected in 1897 (MVZ 116744) and the second from an alcohol-preserved specimen (MVZ 177235). Both of these feathers exhibited aerodynamic behavior and sounds similar to our prior published work on fresh feathers (Clark et al., 2011; Clark and Feo, 2008), suggesting that feathers from old or alcohol-preserved museum specimens have similar material properties, and thus flutter the same, as fresh feathers.

Evolutionary diversity

We compiled a list of taxa reported to produce notable flight sounds from the literature, including descriptions of feathers that may be modified for sound production. We then searched for recordings of flight sounds, from our own field work, the Macaulay Library of Natural Sounds (ML; macaulaylibrary.org), Xeno-Canto (XC; www.xeno-canto.org), the British Library of Wildlife Sounds (BLOWS; bl.uk/collection-guides/wildlife-and-environmental-sounds), the Borror Laboratory of Bioacoustics (blb.osu.edu), commercial compact disks of bird song (references in Table S1) and colleagues. We also searched (in 2010) recording metadata for keywords such as 'wing', 'flight', 'display' and 'flight call'. We haphazardly sampled additional recordings of focal taxa to find examples of flight sounds that had not been indicated in the metadata (primarily recordings from ML and XC). We classified sounds by hypothesized production mechanism, according to their acoustic form.

These natural history data are sparse, providing evidence of the presence, but not evidence of the absence, of sonations. It is also incomplete, in that there must be additional taxa that produce undescribed or unrecorded sonations. These weaknesses would make it misleading to reconstruct the evolutionary origins of feather sonation explicitly.

Despite these limitations, we developed a heuristic, preliminary estimate of the number of evolutionary origins of feather sonation mechanisms, using currently available avian phylogenies (Barker et al., 2004; Hackett et al., 2008; McGuire et al., 2014). We defined an evolutionary origin of sonation mechanism as an independently evolved instance of a specific physical mechanism of sound production in which the sound is apparently modulated or produced intentionally as part of a display. By this definition, any two taxa with different mechanisms of sound production within a display comprised two origins of sonations, even if they were produced in the context of homologous display behaviors. For instance, the hummingbird

genera *Archilochus* and *Selasphorus* produce homologous shuttle display behaviors, but the wing sounds produced during the display by our definition constitute at least two separate origins of sonations, as the mechanism differs: *Archilochus* produce a wing whirring sound apparently with primary feathers P1–P6, whereas *Selasphorus* produce sounds via aeroelastic flutter of outer primaries P9 and P10 (Clark et al., 2012). In grouse, spruce grouse use wing clapping (Boag and Schroeder, 1992), ruffed grouse use pulsed air (Archibald, 1974), Caucasian grouse use aeroelastic flutter (Bergmann et al., 1991) and greater sage-grouse use feather–feather rubbing (Schroeder et al., 1999), constituting four independent origins of different acoustic mechanisms, regardless of the exact phylogenetic relationship among these taxa. Similarly, an individual species can represent multiple origins, as in *Selasphorus* hummingbirds that produce sounds with both the wings (Miller and Inouye, 1983) and the tail (Clark et al., 2012).

For clades with diverse sonations and unresolved phylogenies (e.g. New World flycatchers, nightjars), we conservatively assumed that all taxa that produce sound via the same acoustic mechanism and with the same flight feathers consisted of a single origin of sonation. By contrast, we assumed that distantly related clades in which multiple outgroups were not known to produce sonations constituted independent origins. We then assembled a list of independent origins of sonations using parsimony. Alternative definitions of the origin of sonation, such as based on behavior rather than physical acoustic mechanism, would produce a somewhat different number of inferred origins. For instance, the various sonations in the genus *Cotinga* (Table S3) likely reflect a single behavioral origin. But behavioral definitions of sonations pose other problems, such as problems of homology, that cannot be resolved with our data. For instance, do the snap and roll–snap sonations of *Manacus candei* (Bostwick and Prum, 2003) constitute non-homologous sonations (same acoustic mechanism, somewhat different behavior)? While such a behavioral definition would likely increase the number of inferred origins of sonations in some clades (e.g. hummingbirds, manakins) and decrease them in others (e.g. cotingas), such changes would not affect the general conclusions presented in this paper.

RESULTS AND DISCUSSION

Properties of flutter of individual feathers in the wind tunnel

We tested the aeroelastic flutter hypothesis on one or more feathers from 35 taxa in 14 bird families (listed in Table S2). The feathers varied from 5 to 30 cm in length, where 30 cm was the upper length

limit of the working section of the wind tunnel. As predicted, at sufficiently high airspeeds, all feathers tested were capable of spontaneously fluttering at one or more orientations. This supports our hypothesis that all pennaceous flight feathers have an intrinsic capacity to produce sound via flutter. Most tested feathers produced tonal sound, with fundamental frequencies varying from 0.2 to 10 kHz (Fig. 1). The larger feathers tested tended to exhibit flutter that was chaotic (Alben and Shelley, 2008), rather than a limit cycle, and chaotic flutter does not produce tonal sound. Whether this chaotic flutter was caused or influenced by the limited dimensions of the test section of our wind tunnel was unclear.

The mechanics of flutter in this phylogenetically diverse sample of feathers were similar in many respects to the data explored in detail for hummingbird feathers (Clark et al., 2013a,b, 2011). For instance, all feathers in limit cycle oscillations (stable oscillatory motion always easily visible in high-speed video) produced strong integer harmonic frequencies, including common snipe (*Gallinago gallinago*) outer tail feathers (Fig. 2A,B). These results support the prediction of aeroelastic flutter as the driving mechanism, and not the vortex-induced vibration hypothesis proposed by van Casteren et al. (2010) for common snipe feathers. The vortex model predicts a strong, linear, positive relationship between oscillation frequency and airspeed and it does not predict strong harmonics (Clark et al., 2013b). The first prediction is supported by less than half the feathers (e.g. Fig. 2B) but not by the others (e.g. Fig. 2D), and the second prediction is not supported by the wind tunnel data for any feather we measured, including snipe (Figs 1, 2). van Casteren et al. (2010) state that the common snipe feathers they tested in a wind tunnel did not produce harmonics. Yet, this species produces prominent harmonics during its display (Fig. 2A), as did the snipe tail feathers tested here (Fig. 2B) and in a prior study (Reddig, 1978). This means that, per our criterion 1, van Casteren et al.'s (2010) empirical data did not replicate the sounds actual snipe make. For this reason, along with criticisms mentioned in Clark et al. (2013b), we suggest that van Casteren et al.'s (2010) conclusion that shed vortices cause sound production is not supported for snipe, or for any feather measured thus far.

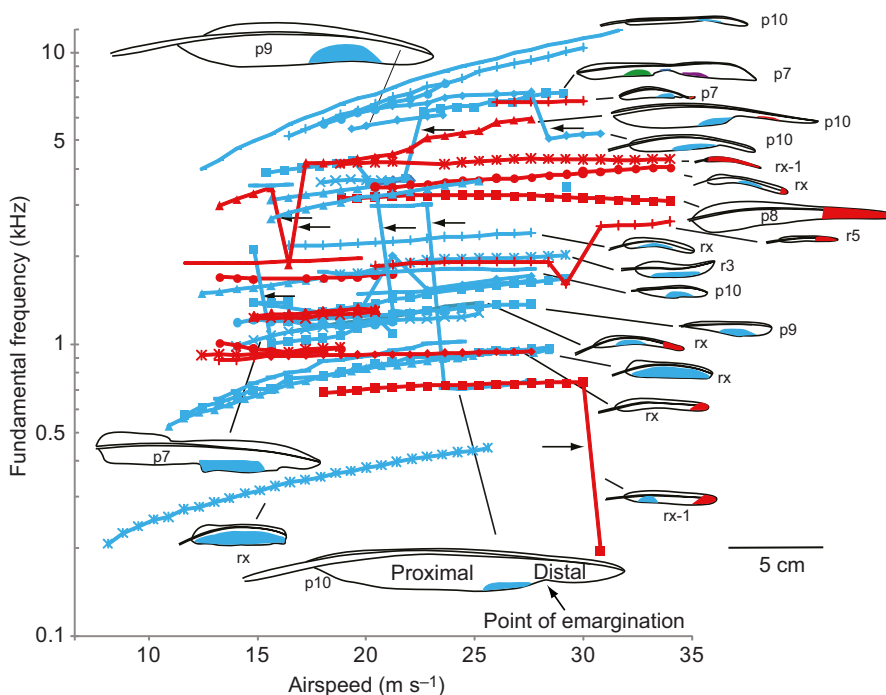


Fig. 1. Flutter fundamental frequency plotted against airspeed for 43 flight feathers tested in a wind tunnel. Some feather outlines are not shown here but are presented in an expanded version of this figure (see Fig. S1). Illustrations of individual feathers are drawn to scale (5 cm scale bar). Color patches show approximate regions of flutter and mode of flutter: red, tip mode; blue, trailing vane mode; green and purple indicate additional modes expressed simultaneously at alternative frequencies. Arrows indicate abrupt changes in frequency caused by flutter 'jumping' from one mode to another (some mode jumps are not indicated, to reduce clutter). See Fig. S1 for species identity of each feather. Letter/number indicates feather ID: p, primary (wing) feather; r, rectrix (tail feather); snipe have variable numbers of tail feathers (Tuck, 1972), so rx is the outer tail feather and rx-1 is the second to outer tail feather.

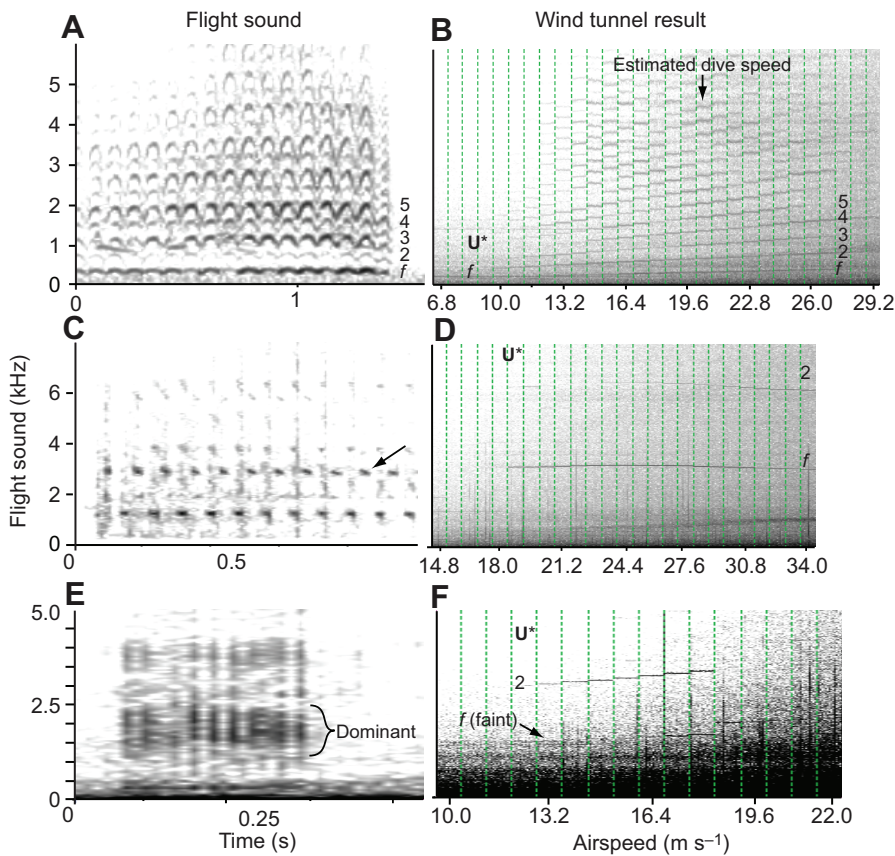


Fig. 2. Spectrograms of flight sounds (left) and sounds produced by individual feathers in the wind tunnel as a function of airspeed (right). (A,B) Male common snipe (*Gallinago gallinago*) 'winnowing' display flight (B, outer tail feather). (C,D) Crested pigeon (*Ocyphaps lophotes*) taking flight (Hingee and Magrath, 2009) (D, wing feather P8). (E,F) Male Puerto Rican tody (*Todus mexicanus*) wing whirr. In common snipe (A,B) and crested pigeon (C,D), aeroelastic flutter is supported as the mechanism generating the flight sound: the sound is tonal and the fundamental frequency of sound (f) produced in the wind tunnel matches that of the bird. By contrast, the 'wing whirring' sounds of the Puerto Rican tody (E,F) are not as tonal (pulses are at the wingbeat frequency). Though the fundamental frequency of flutter in the wind tunnel (arrow in F) is similar to the dominant frequency of the flight sound, the sound in the tunnel was weak (hence a harsher contrast of spectrogram) and difficult to elicit, causing us to reject the flutter hypothesis as the mechanism producing this type of sound. U^* indicates the minimum airspeed for aeroelastic flutter; 2nd–5th integer harmonics are numbered. Wind tunnel spectrograms depict a series of measurements separated by dashed lines that were each taken at fixed airspeed.

Although the feathers we tested were of diverse shapes (Fig. 1; Fig. S1), all modes of flutter elicited were tip or trailing vane modes, as categorized by the region of the feather that was aerodynamically activated. The mode shape (i.e. the spatial distribution of motion across the feather) of flutter varied among the feathers sampled. Because of variation in mode shape, feather size did not exhibit a tight negative correlation with sound frequency (Fig. 1), as might be expected from simple allometry of how feather resonance modes ought to scale with size (Clark et al., 2013a). Rather, large feathers tended to flutter with a proportionally small fraction of their vane surface area. Thus, large feathers may nonetheless produce high-pitched sound, just as small feathers may in some circumstances produce low-pitched sound (Clark et al., 2013b).

Airspeed had a variable influence on the sound produced by flutter (Fig. 1), similar to findings with hummingbird feathers (Clark et al., 2013a,b). In feathers of some taxa, such as some snipe, frequency increased proportionately with airspeed (Fig. 2B). But in a few cases, such as crested pigeon P8, frequency actually slightly declined with increasing airspeed (Fig. 2D). This has implications for potential communication function. The variable frequency–velocity relationship in snipe (Fig. 1, Fig. 2B) (Reddig, 1978) means that in the winnowing display, pitch is an index signal for male display flight speed (arrow in Fig. 2B), whereas sound frequency is not an index of flight speed in crested pigeon (Fig. 2C,D).

Multiple types of non-linearities in feather flutter can occur as a function of airspeed. Mode jumps, in which the feather abruptly shifted from one limit cycle oscillation, with a particular mode shape, into another (arrows in Fig. 1) were common. Occasionally, we observed harmonic dominance, in which a harmonic contained more energy than the fundamental frequency (Fig. 2D at speeds above 30 m s^{-1}), a feature occasionally present in a few sonations, such as those of some snipe.

Flutter and the flight sounds of birds

Our literature and sound library survey revealed that distinctive flight sounds featured during either ordinary flight or specialized displays are produced by members of most orders of birds (Table S1). Many of these flight sounds are tonal. They are characterized by a narrow frequency range (normally of $<0.1 \text{ kHz}$ bandwidth) and integer-multiple harmonics (Fig. 2A,C). While these sounds often superficially resemble the high-pitched, tonal sound of a whistle, tonal flight sounds may also sound 'buzzy' on account of their harmonics, akin to the sound produced by a flying bee, as in many hornbills, when the tone is low pitched and has strong harmonics. In addition to well-known tonal flight sounds such as those of ducks or doves, we found many little-known examples produced in ordinary flight, such as in cormorants, ravens, ptarmigan and others (Table S1). These sounds are not short, percussive (impulsive) sounds, and can last for seconds in some flight contexts, such as the sound of a hornbill gliding to a perch (Audio 6). This last feature implies these sounds are produced by steady-state oscillations. Birds that ordinarily have relatively quiet flight may produce incidental tonal sounds during molt, when missing an outer primary feather (great-tailed grackle and various hummingbirds; C.J.C., personal observation). Molt creates temporary gaps between flight feathers that may free an inner vane of a feather to flutter and produce sound, which it would not be free to do when the wing was full-feathered. In addition to tonal flight sounds produced during ordinary locomotion, we found many little-known examples of non-vocal sounds produced in displays, such as African pitta (*Pitta angolensis*), lesser florican (*Sypheotides indicus*) or red phalarope (*Phalaropus falcarius*) (Table S1).

The tonality of many of these sounds, both specialized sounds from ordinary locomotion and those produced during display, are broadly consistent with the sounds fluttering feathers produced in the

wind tunnel. So, we tested whether aeroelastic flutter induced in a wind tunnel by a diverse array of feathers in fact matched the tonal flight sounds of these species. Following our four criteria (see Introduction), we reproduced sounds in the wind tunnel that matched wild flight sounds of 15 species from six families (Table S2), including sounds of lyre-tailed honeyguide (*M. robustus*), multiple snipe (*Gallinago* spp.), scissor-tailed flycatcher (*Tyrannus forficatus*) and crested pigeon (*Ocyphaps lophotes*). The flutter sounds we induced in the wind tunnel did not match wild flight sounds for feathers from an additional 20 species from 11 families.

We hypothesize that half of these negative results are false negatives. Many of our tests were conducted on feathers that lacked any obvious modifications in shape. Feathers of six species in this category, including most duck feathers, failed to replicate the acoustic quality of the flight sound recordings of these species. In these species, we tested one or more emarginated outer primary feathers (Fig. 1), because emargination causes the feather tips to separate in flight, a feature we hypothesized would allow flutter in the regions distal to the point of emargination (Feo and Clark, 2010). But this hypothesis was largely unsupported: in the wind tunnel, unmodified, emarginated feathers tended to flutter proximal to the point of emargination (Fig. 1), where the vane is thinner, less stiff, and seems designed to overlap with the neighboring feathers. As a result, we propose that negative results in these species have a simple explanation: we likely tested the wrong wing feathers. The acoustic qualities of the flight sounds produced by taxa such as ducks are highly tonal and fully consistent with flutter, and not with another described aeroacoustic mechanism (see discussion of wing whirring, below). Thus, we predict that in these six species, future work will find that these tonal sounds are in fact produced by flutter.

This result, that unmodified emarginated feathers tended to flutter proximal to the point of emargination, does not imply that an emarginated shape is entirely unrelated to sound production. The highly modified, sharply emarginated, sexually dimorphic P10 of scissor-tailed flycatcher (*T. forficatus*; feather e in Fig. S1) produced loud sounds matching the flight sound, by flutter of the emarginated region. The other emarginated feathers we tested were not as clearly modified for sound production. Thus, the portion of an individual feather or wing most prone to flutter may not be easily identified from morphology alone.

The other hypothesized false negatives come from cases in which multiple feathers together may act as the sound source. If this is the case, wind tunnel tests of a single feather, as done here, would be insufficient to duplicate the sounds experimentally (Clark, 2014). We tested feathers from four clades that had modified feathers from inside the wing (P7 or P8), in which a gap forms between neighboring feathers: red cotingas (*Phoenicercus* spp.), little bustard (*Tetrax tetrax*), crested pigeon (*O. lophotes*) and tui (*Prosthemadera novaeseelandiae*). Of these, we only replicated the flight sound produced by crested pigeon (Fig. 2C,D). For the four species from the other three clades, we posit that the flight sound production requires an interaction with neighboring feathers that our experimental setup failed to reproduce (Table S2). Moreover, crested pigeon actually produces two tones, one on the downstroke, the other on the upstroke (Hingee and Magrath, 2009). Our wind tunnel experiments on P8 replicated only the higher sounds (arrow in Fig. 2C), meaning this single feather did not replicate the flight sound in its entirety.

Whirring sounds

For the other 10 species that failed to reproduce the flight sound in the wind tunnel (Table S2), we propose these are true negative

results, i.e. the flight sound in question is not produced by aeroelastic flutter. In addition to the four mechanisms recognized in the Introduction, we call this previously unrecognized mechanistic category of feather sound production ‘wing whirring’ (Fig. 2E; e.g. Cuban tody in Audio 9; vermilion flycatcher in Audio 10). Previously, this term has been used to loosely refer to either kinematics or acoustics of feather sounds. Wing whirring as a category includes the snorts and rattles of *Manacus* manakins (Bostwick and Prum, 2003).

Acoustically, wing whirring sounds are intermediate between flutter-induced tones and claps/snaps. Many sound like a dry, atonal version of a rolled ‘rr’ sound. Wing whirrs consist of a series of pulses, each individual pulse coinciding with a fraction of a wingbeat, which we hypothesize is usually the downstroke. The time course is not as short and impulsive as a snap or clap, allowing us to reject percussion as the mechanism. They also have limited frequency bandwidth, sometimes approaching the narrow bandwidth of tonal flight sounds, though integer harmonics are typically weak or absent. The sounds that feathers of these species produced in the wind tunnel in no way replicated the display sounds of the actual birds, per our four criteria. For instance, Puerto Rican tody (*Todus mexicanus*) males produce a wing whirr in flight during territorial interactions with other males (Fig. 2E). The frequency of flutter of the primary feather we tested was approximately the same as the peak frequency of the wing whirr (Fig. 2F). But, flutter was difficult to elicit from this feather, was quiet, and had a much narrower bandwidth than the sonation, such that the sounds we elicited from the feather in the tunnel did not sound like the sonation produced by the bird, thus failing criterion 4. It also may have failed criterion 2; flutter only occurred above 12 m s^{-1} , an airspeed that may exceed the wingtip velocity of todies, which are small, slow-flying forest birds.

The physical mechanisms that produce these wing whirring sounds remain unknown. These sounds are produced only during active flapping, and we have no examples of them being produced by the tail or during gliding flight (Table S1). As the wind tunnel tests were in non-accelerating conditions, we propose these sounds arise from some sort of dynamic (i.e. involving acceleration) interaction between primary feathers during the downstroke (Bostwick and Prum, 2003) that our wind-tunnel tests did not replicate.

Evolution of non-vocal communication in birds

In addition to flutter and wing whirring sounds, our review of literature and sound archives for non-vocal avian sounds identified many displays with sounds consistent with feather or wing percussion (snaps and claps), including displays of owls, hummingbirds, long-tailed ground roller (Tobias and Seddon, 2003), Arctic warbler (Lowther and Sharbaugh, 2008) and many others (Tables S1, S3). Several additional physical acoustic mechanisms of communication sounds are rare among birds. Stridulation is apparently unique to club-winged manakin (*Machaeropterus deliciosus*) (Bostwick and Prum, 2005) and possibly derived from percussion (Kimberly Bostwick and R.O.P., unpublished data). The ‘drumming’ sounds of ruffed grouse (*Bonasa umbellus*) (Archibald, 1974) and white-winged nightjar (*Eleothreptus candicans*) are atonal and low frequency, and the precise aeroacoustic mechanism is unclear (labeled ‘air pulse’ in Fig. 3). Some manakins produce whooshes (Bostwick and Prum, 2003; DuVal, 2007; Prum, 1998) or rustling (Bostwick and Prum, 2003) apparently as communicative sounds, and magnificent riflebird (*Ptiloris magnificus*) also produces rustling sounds during display (ML 455444). Greater sage-grouse (*Centrocercus urophasianus*) rub their wings against bristly chest feathers via some

sort of feather–feather contact mechanism (Koch et al., 2015) that is possibly derived from rustling.

In the absence of a fully resolved phylogeny of birds and better data on the absence of non-vocal feather sounds in birds (see

Materials and methods), we used recent phylogenies of birds (Barker et al., 2004; Hackett et al., 2008) and simplifying assumptions about the evolution of non-vocal sounds within avian families to make a heuristic estimate of the number of evolutionary origins of non-vocal communication sound production in living birds. Although we have high confidence in the presence of non-vocal communication sounds widespread in birds (presented in full in Table S1), the lack of accurate absence data makes a detailed phylogenetic analysis problematic (Areta and Miller, 2014). Our analysis implies that there are numerous evolutionarily independent origins of mechanisms of non-vocal communication (Fig. 3; Tables S1, S3).

All birds, even owls (Sarradj et al., 2011), produce some sort of acoustic signature in flight. Out of these ubiquitous non-functional sounds, birds have apparently evolved mechanisms of feather sonation ~69 or more times (Fig. 3; Table S3). Among these 69 proposed origins, three physical mechanisms appear to be widespread and frequently convergently evolved. Flutter-induced feather sounds appear to have evolved as communication signals at least 27 times in birds of at least nine orders (Fig. 3; Tables S1, S3). Wing whirring appears to have evolved a minimum of 11 times, including in the sickle-winged nightjar, gnateaters (*Conopophaga*), some cotingas, todies, manakins and tyrannid flycatchers (Fig. 3). Snaps/claps have evolved as communication sounds in displays at least 24 times, while the various rare mechanisms combined account for at least seven evolutionary origins. As described further in the Materials and methods, these origins include instances in which one physical mechanism (e.g. percussion in manakins) has transformed into another (e.g. stridulation of club-winged manakin). Some mechanisms of incidental flight sounds have evolved into communication signals more frequently than others. Aeroelastic flutter, percussion and wing whirring have repeatedly evolved into non-vocal communication sounds, whereas whooshes and rustling sounds seem relatively rare as signals, even though they are ubiquitous as adventitious sounds during ordinary flight (Fig. 3; Table S1).

Most sonations are produced by the wings (65 out of 69) and when airborne (including jump displays; Table S3). Only four clades are known to generate sounds with the tail (bee hummingbirds, snipe, lyre-tailed honeyguide and *Heterocercus* manakins), and in all four instances, this occurs during a gravity-powered, high-speed dive.

Several clades have especially high diversity of feather sonations and sonation mechanisms: hummingbirds, nightjars, cotingas, manakins, New World flycatchers, gallinaceous birds and shorebirds (Fig. 3). In all but two of the origins hypothesized, the sounds are likely to be secondary sexual characters, as they are produced primarily by males, or by females in the sex-role reversed red phalarope. Typically, they are produced during the breeding season only, such as during courtship displays that are directed to a female, or in replacement of vocal song that is broadcast into the environment, indicating sexual function. In the other two cases, crested pigeon and golden-bellied starfrontlet (*Coeligena bonapartei*), both sexes produce the sound and the inferred function is non-sexual communication (Hingee and Magrath, 2009). Hummingbirds, nightjars and tyrant flycatchers all forage in flight, which may make them more likely to produce incidental sounds that are subject to subsequent sexual selection, in much the same way that foraging on insects in wood must have contributed to the evolution of drumming signals in woodpeckers (Picidae).

Conclusions

The data presented here support Darwin's (1871) hypothesis that avian feather sounds evolve most frequently by intersexual selection

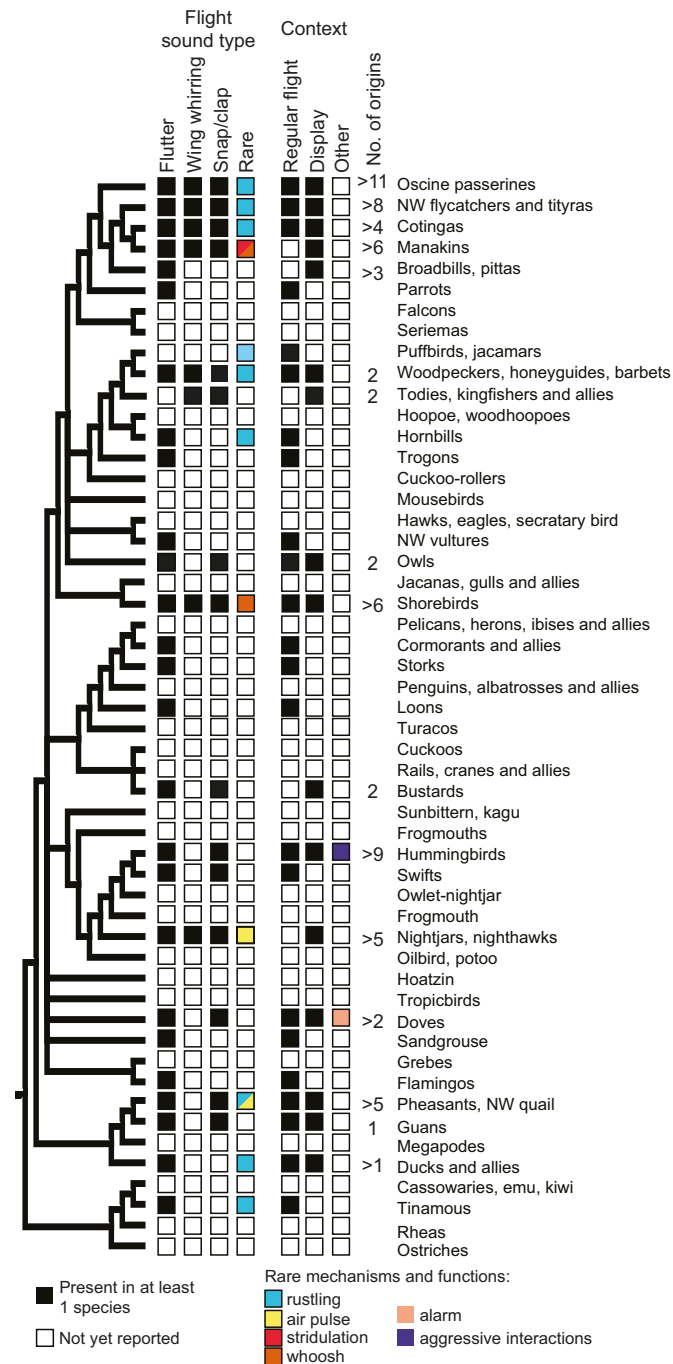


Fig. 3. Major clades of birds with occurrences of different mechanisms of flight sounds, and their inferred function. Phylogeny modified from Barker et al. (2004) and Hackett et al. (2008). Black box indicates at least one species within the clade produces sound of a particular mechanism and function; white box indicates no reports from that clade, but does not necessarily reflect true absence. In no clades marked as present are sonations universally reported. Number of origins refers to hypothesized independent origins of wing or tail feather sonation mechanisms, which have independently evolved more than 69 times in birds. Inferred origins are listed individually in Table S3. NW, New World.

or mate choice. In 67 of 69 independent origins of sonation mechanisms we have proposed (Table S3), sonations are secondary sexual characters, and clades with high diversity of these sounds tend to contain lekking species with acrobatic displays. Two factors appear to promote this evolutionary pattern: the active nature of displays lends itself to incidental sound production (Prum, 1998), and some mechanisms of sound production are evolutionarily labile. Courtship displays can be dynamic and active, meaning that incidental sounds of locomotion are likeliest or loudest during these behaviors (Prum, 1998), much as human running is louder than walking. Three mechanisms, aeroelastic flutter, percussion and wing whirring, together account for the majority of non-vocal communicative sounds in birds, perhaps because they are acoustically labile, and easily evolved from a byproduct of a vigorous motion into novel acoustic stimuli. By contrast, we propose that the mechanisms generating whooshes and rustling sounds are a poor fit to Darwin's second criterion, that simple changes in morphology or behavior readily produce significant changes in the acoustic form of the sound. Accordingly, there may be reduced physical capacity for selection to elaborate these sounds.

As the crunch of leaves underfoot or footsteps in a hallway show, all locomotion intrinsically generates sound. Whereas locomotion-induced sound of terrestrial animals varies with substrate (Elias et al., 2005; Randall, 2001), the properties of air are relatively invariant. Thus, the acoustic signature of animal flight reveals aerodynamic processes in play over their wing and tail feathers, such as turbulence-induced whooshes, aeroelastic flutter and the associated tonal flight sounds; and the poorly understood mechanism(s) that produce wing whirring. The acoustic signature of flutter, tonal sound, is widespread in the ordinary flight of many birds. The sounds produced by feather flutter also evolve through selection, as its acoustic properties (pitch, loudness, harmonic structure) are easily modified by small changes in either feather morphology or behavior (Fig. 1).

Finally, our conclusion that feather flutter is widespread in bird flight would seem to have implications for the mechanics of bird flight. In airplanes, flutter modes elicited tend to incorporate a large portion of the wing, produce a large increase in drag, and often cause the wing to break catastrophically (Bisplinghoff et al., 1996). Bird wings, in contrast, are composed of many individual feathers, resulting in structural isolation of parts that may be prone to flutter. Modes of flutter therefore involve a smaller fraction of the wing surface in birds. Feathers also can withstand high strain, which may be why we know of few examples suggesting flutter-induced damage to feathers (but see Miskelly, 1990). If only a small region of a wing flutters, the accompanying increase in drag may also be small. For birds such as ducks and doves that tend to produce these sounds in ordinary flight, the drag caused by flutter may pose a small aerodynamic penalty that does not offset other advantages of the morphology.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

C.J.C. and R.O.P. designed the study. C.J.C. collected and analyzed the data. C.J.C. and R.O.P. wrote the manuscript.

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Supplementary information

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