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RESEARCH ARTICLE

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

Christopher J. Clark*,‡ and Richard O. Prum

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 thorntail 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.

Department of Ecology & Evolutionary Biology, and Peabody Museum of Natural History, Yale University, New Haven, CT 06511, USA.
*Present address: Department of Biology, University of California, Riverside, CA 92521, USA.

‡Author for correspondence (cclark@ucr.edu)

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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

Journal of Experimental Biology

Journal of Experimental Biology (2015) 218, 3520-3527 doi:10.1242/jeb.126458

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.

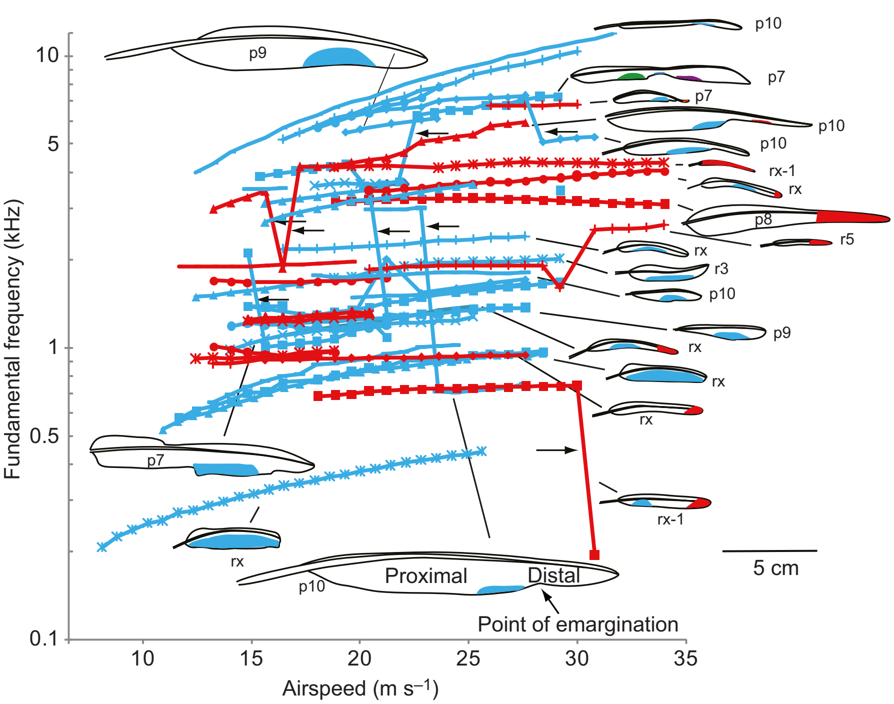

Fig. 1. Flutter fundamental frequency plotted against airspeed for 43 flight feathers tested in a wind tunnel. Some feather outlines are not shown here but are presented in an expanded version of this figure (see Fig. S1). Illustrations of individual feathers are drawn to scale (5 cm scale bar). Color 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.

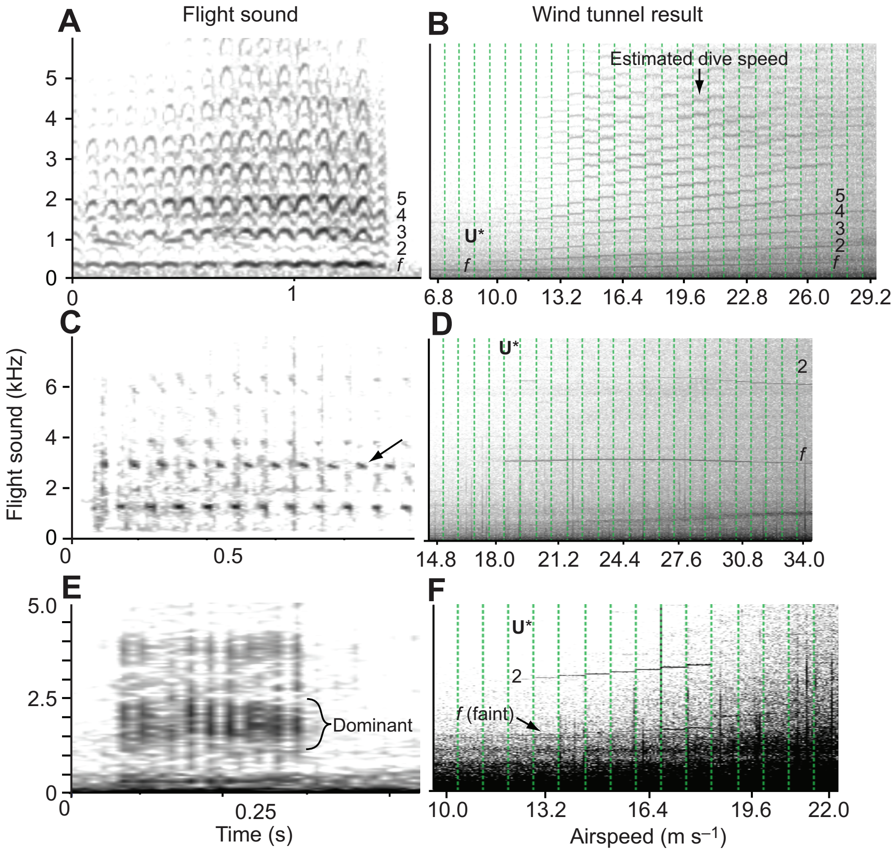

Fig. 2. Spectrograms of flight sounds (left) and sounds produced by individual feathers in the wind tunnel as a function of airspeed (right). (A,B) Male common snipe (*Gallinago gallinago*) 'winnowing' display flight (B, outer tail feather). (C,D) Crested pigeon (*Ocyphaps lophotes*) taking flight (Hingee 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 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 falicarius*) (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

Journal of Experimental Biology (2015) 218, 3520-3527 doi:10.1242/jeb.126458

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; vermillion 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).

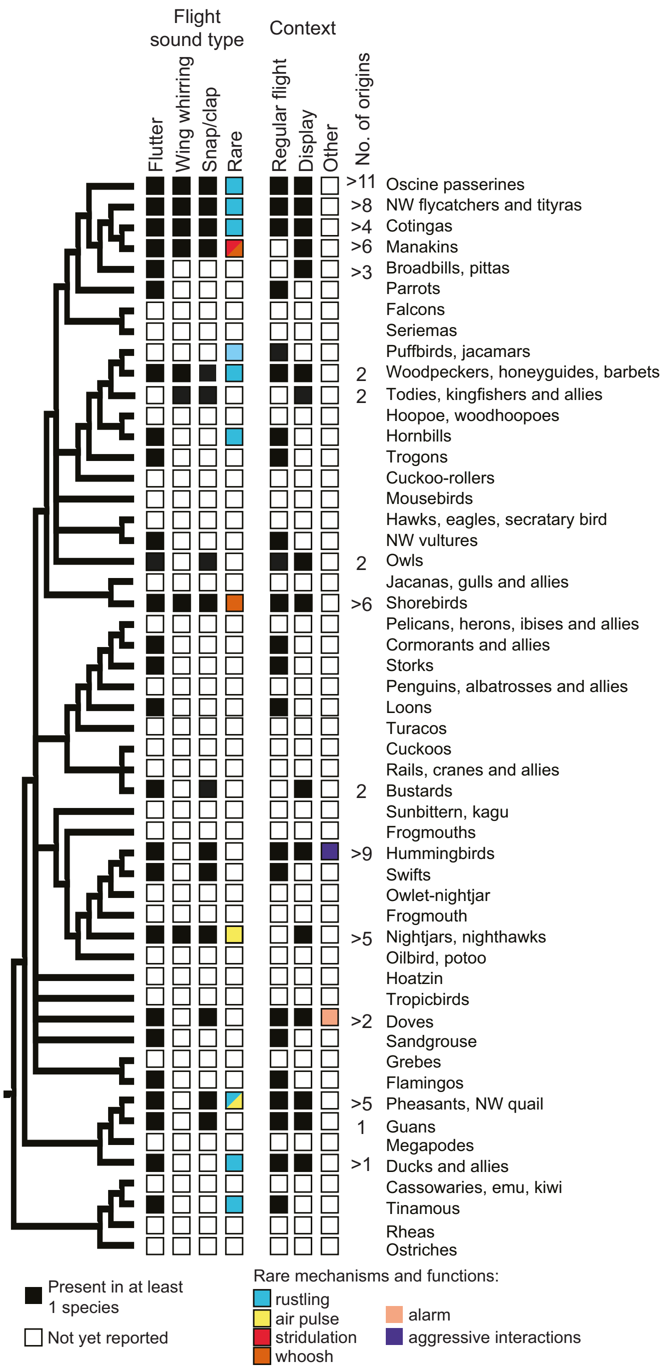

Fig. 3. Major clades of birds with occurrences of different mechanisms of flight sounds, and their inferred function. Phylogeny modified from Barker et al. (2004) and Hackett et al. (2008). Black box indicates at least one species within the clade produces sound of a particular mechanism and function; 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.

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 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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Table S1. Birds that produce sounds with the wings or tail, not including turbulence-induced whooshes or humming.

Order	Family	Genus	Species	Mechanism[1]	Context[2]	Sound example[3]	Citation
Tinamiformes	Tinamidae	*Nothura*	*spp*	AF, RU	Flight	ML 20279, XC 23843	(Sick, 1993)
Anseriformes	Anatidae	*Aix*	*sponsa*	AF	Flight	(Oberle, 2008)	
Anseriformes	Anatidae	*Anas*	*acuta*	AF	Flight, Display	BL 29802	(Manson-Bahr and Pye, 1985)
Anseriformes	Anatidae	*Anas*	*americana*	AF	Flight	BL 780	
Anseriformes	Anatidae	*Anas*	*capensis*	AF	Flight	ML 2494	
Anseriformes	Anatidae	*Anas*	*clypeata*	AF	Flight, Display	XC 42544	(Dubowy, 1996; McKinney, 1970)
Anseriformes	Anatidae	*Anas*	*crecca*	AF	Flight		(Manson-Bahr and Pye, 1985)
Anseriformes	Anatidae	*Anas*	*discors*	AF	Flight	ML66879	
Anseriformes	Anatidae	*Anas*	*erythrorhyncha*	AF	Flight	ML3414	
Anseriformes	Anatidae	*Anas*	*flavirostris*	AF	Flight	ML58953	
Anseriformes	Anatidae	*Anas*	*fulvigulata*	AF	Flight	BL26460	
Anseriformes	Anatidae	*Anas*	*georgica*	AF	Flight	XC32168	
Anseriformes	Anatidae	*Anas*	*platychynchos*	AF	Flight	XC25717	
Anseriformes	Anatidae	*Anas*	*puna*	AF	Flight	XC15477	
Anseriformes	Anatidae	*Anas*	*rubripes*	AF	Flight	ML49718	
Anseriformes	Anatidae	*Anas*	*smithii*	AF	Flight	(Gibbon, 2003)	
Anseriformes	Anatidae	*Anas*	*strepera*	AF	Flight	XC26959	
Anseriformes	Anatidae	*Aythya*	*affins*	AF	Flight	(Oberle, 2008)	
Anseriformes	Anatidae	*Beucephala*	*albeola*	AF	Flight	ML57549	
Anseriformes	Anatidae	*Beucephala*	*clangula*	AF	Flight	XC11501	(Lucas and Stettenheim, 1972; Manson-Bahr and Pye, 1985)
Anseriformes	Anatidae	*Beucephala*	*islandica*	AF	Flight	ML60522	
Anseriformes	Anatidae	*Branta*	*ruficollis*	AF	Flight	(Zöchler, 2007)	

Journal of Experimental Biology • Supplementary information

Anseriformes	Anatidae	*Clangula*	*hyemalis*	AF	Flight	BL20830	
Anseriformes	Anatidae	*Cygnus*	*bewicki*	AF	Flight	(Ueda, 1999)	
Anseriformes	Anatidae	*Cygnus*	*buccinator*	AF	Flight	ML130982	
Anseriformes	Anatidae	*Cygnus*	*columbianus*	AF	Flight	BL28011	
Anseriformes	Anatidae	*Cygnus*	*melancoryphus*	AF	Flight	XC15127	(Sick, 1993)
Anseriformes	Anatidae	*Cygnus*	*olor*	AF	Flight	ML3763	(Kear, 2005; Manson-Bahr and Pye, 1985)
Anseriformes	Anatidae	*Dendrocygna*	*arcuata*	UNCLEAR	Flight		Kear 2005
Anseriformes	Anatidae	*Dendrocygna*	*bicolor*	AF	Flight	ML97450	
Anseriformes	Anatidae	*Dendrocygna*	*eytoni*	AF	Flight		Kear 2005
Anseriformes	Anatidae	*Dendrocygna*	*guttata*	AF	Flight		Kear 2005
Anseriformes	Anatidae	*Dendrocygna*	*javanica*	AF	Flight		(Lucas and Stettenheim, 1972)
Anseriformes	Anatidae	*Dendrocygna*	*viduata*	AF	Flight	ML97442	Sick 1993
Anseriformes	Anatidae	*Lophodytes*	*cucullatus*	AF	Flight	ML61563	
Anseriformes	Anatidae	*Melanitta*	*fusca*	AF	Flight	ML42997	
Anseriformes	Anatidae	*Melanitta*	*nigra*	AF	Flight	ML130900	Lucas and Stettenheim 1972
Anseriformes	Anatidae	*Melanitta*	*perspicillata*	AF	Flight	BL23918	
Anseriformes	Anatidae	*Nettapus*	*pulchellus*	RU	Flight	CD	
Anseriformes	Anatidae	*Tadorna*	*ferruginea*	AF	Flight	XC30167	
Anseriformes	Anatidae	*Tadorna*	*tadorna*	AF	Flight		(Manson-Bahr and Pye, 1985)
Galliformes	Cracidae	*Aburria*	*aburri*	S/C?	Display	ML64085	(Delacour and Amadon, 1973)
Galliformes	Cracidae	*Aburria*	*pipile*	S/C?	Display	ML25289	(Delacour and Amadon, 1973)
Galliformes	Cracidae	*Chamaepetes*	*goudotii*	S/C	Display	XC21110	
Galliformes	Cracidae	*Chamaepetes*	*unicolor*	S/C?	Display	XC21110	(Darwin, 1871; Delacour and Amadon, 1973);
Galliformes	Cracidae	*Crax*	*globulosa*	S/C	Display		(Vaurie, 1968)
Galliformes	Cracidae	*Penelope*	*argytotis*	S/C?	Display	ML67945	

Galliformes	Cracidae	*Penelope*	*barbata*	S/C?	Display	ML21914	
Galliformes	Cracidae	*Penelope*	*jacquacu*	S/C?	Display	ML67643	
Galliformes	Cracidae	*Penelope*	*marail*	S/C?	Display	ML67615	
Galliformes	Cracidae	*Penelope*	*montagnii*	S/C?	Display	ML64009	
Galliformes	Cracidae	*Penelope*	*obscura*	S/C?	Display	ML18867	(Delacour and Amadon, 1973)
Galliformes	Cracidae	*Penelope*	*ortoni*	S/C?	Display	(Jahn et al., 2003)	
Galliformes	Cracidae	*Penelope*	*purpurascens*	AF, S/C?	Flight, Display	ML63693	Vaurie 1968
Galliformes	Cracidae	*Penelopina*	*nigra*	S/C?	Display	ML55402	(Delacour and Amadon, 1973)
Galliformes	Cracidae	*Pipile*	*cujubi*	S/C?	Display	XC3274	
Galliformes	Odontophoridae	*Colinus*	*cristatus*	AF	Flight	(Alvarez et al., 2007)	
Galliformes	Odontophoridae	*Cyrtonyx*	*montexumae*	AF	Flight	XC34437	
Galliformes	Phasianidae	*Bonasa*	*umbellus*	MISC	Display	ML2384	(Manson-Bahr and Pye, 1985)
Galliformes	Phasianidae	*Centrocercus*	*urophasianus*	MISC	Display	ML 126562	(Schroeder et al., 1999)
Galliformes	Phasianidae	*Falcipennis*	*canadensis*	S/C	Display	Youtube	(Boag and Schroeder, 1992)
Galliformes	Phasianidae	*Lagopus*	*lagopus*	AF, RU	Flight	ML105848	(Manson-Bahr and Pye, 1985)
Galliformes	Phasianidae	*Lagopus*	*mutus*	AF, RU	Flight	ML62346	(MacDonald, 1970)
Galliformes	Phasianidae	*Pavo*	*cristatus*	MISC	Display		Hare, pers. comm.
Galliformes	Phasianidae	*Perdix*	*perdix*	RU	Flight		(Manson-Bahr and Pye, 1985)
Galliformes	Phasianidae	*Phasianus*	*colchicus*	AF, S/C	Flight	XC29209	(Manson-Bahr and Pye, 1985)
Galliformes	Phasianidae	*Tetrao*	*mlokosiewiczi*	AF	Display		(Bergmann et al., 1991)
Charadriformes	Alcidae	*Brachyramphus*	*marmoratus*	AF, MISC?	Flight	ML 84257, ML 84254	(Nelson and Hamer, 1995)
Charadriformes	Charadriidae	*Charadrius*	*bicinctus*	S/C	Display		(Bomford, 1986)
Charadriformes	Charadriidae	*Vanellus*	*vanellus*	AF	Display	BLOWS: BLW VANELLUS VANELLUS R3 C22	(Dabelsteen, 1978)
Charadriformes	Scolopacidae	*Calidris*	*alpina*	AF?	Flight	ML138127	(Brown, 1938; Manson-Bahr

							and Pye, 1985)
Charadriformes	Scolopacidae	*Coenocorypha*	*aucklandica*	AF	Display		(Miskelly, 1990; Miskelly, 2005)
Charadriformes	Scolopacidae	*Coenocorypha*	*pusilla*	AF	Display	Miskelly pers. comm.	(Miskelly, 1990)
Charadriformes	Scolopacidae	*Gallinago*	*andina*	AF	Display	XC8502	
Charadriformes	Scolopacidae	*Gallinago*	*delicata*	AF	Display	XC13808	
Charadriformes	Scolopacidae	*Gallinago*	*gallinago*	AF	Display	XC133317	(Carr-Lewty, 1943; Reddig, 1978; Sutton, 1981; Tuck, 1972)
Charadriformes	Scolopacidae	*Gallinago*	*hardwickii*	AF	Display	ML3149	(Nakamura and Shigemori, 1990)
Charadriformes	Scolopacidae	*Gallinago*	*imperialis*	AF	Display	XC6653	
Charadriformes	Scolopacidae	*Gallinago*	*jamesoni*	AF	Display	XC2014	
Charadriformes	Scolopacidae	*Gallinago*	*macrodactyla*	AF	Display	ML93105	
Charadriformes	Scolopacidae	*Gallinago*	*megala*	AF	Display	(Schulze and Dingler, 2007)	(Lucas and Stettenheim, 1972)
Charadriformes	Scolopacidae	*Gallinago*	*nemoricola*	AF	Display	ML3150	
Charadriformes	Scolopacidae	*Gallinago*	*nigripennis*	AF	Display	ML3151	(Taylor, 1925)
Charadriformes	Scolopacidae	*Gallinago*	*nobilis*	AF	Display	XC35088	
Charadriformes	Scolopacidae	*Gallinago*	*paraguaiae*	AF	Display	ML67992	
Charadriformes	Scolopacidae	*Gallinago*	*stenura*	AF	Display	(Zöchler, 2007)	(Byrkjedal, 1990)
Charadriformes	Scolopacidae	*Gallinago*	*undulata*	AF	Display	ML102340	Sick, 1993
Charadriformes	Scolopacidae	*Numenius*	*arquata*	RU	Flight	XC25103	
Charadriformes	Scolopacidae	*Numenius*	*minutus*	AF, RU	Display	BLOWS: BLW NUMENIUS MINUTUS R1 C4	(Labutin et al., 1982)

Charadriformes	Scolopacidae	*Phalaropus*	*fulicarius*	AF	Display	BLOWS: BL W PHALAROPUS FULICARIUS R1 C4	
Charadriformes	Scolopacidae	*Pluvialis*	*apricaria*	UNCLEAR	Display		(Brown, 1938)
Charadriformes	Scolopacidae	*Scolopax*	*minor*	AF	Display	ML94216	(Manson-Bahr and Pye, 1985; Sheldon, 1967)
Gaviiformes	Gavidae	*Gavia*	*immer*	AF	Flight	BL10881	
Gaviiformes	Gavidae	*Gavia*	*pacifica*	AF	Flight	ML131289	
Gaviiformes	Gavidae	*Gavia*	*stellata*	AF	Flight	(Zöchler, 2007)	(Manson-Bahr and Pye, 1985)
Pelecaniformes	Phalacrocoracidae	*Phalacrocorax*	*auritus*	AF	Flight	CJC unpubl. recording	
Pelecaniformes	Phalacrocoracidae	*Phalacrocorax*	*brasilianus brasilianus*	AF	Flight	(Coopmans et al., 2004)	
Ciconiformes	Ciconiidae	*Mycteria*	*americana*	AF	Flight	ML135422	(Kahl, 1972; Manson-Bahr and Pye, 1985)
Cathartiformes	Cathartidae	*Coragyps*	*atratus*	AF	Flight	(Moore et al., 2009); ESM this study	
Phoenicopteriformes	Phoenicopteridae	*Phoenicopterus*	*ruber*	AF	Flight	CJC pers. obvs	
Gruiformes	Otididae	*Ardeotis*	*nigriceps*	UNCLEAR	Display		(Darwin, 1871)
Gruiformes	Otididae	*Sypheotides*	*indica*	S/C?	Display	(Bhatt and Bardolia, 2006)	(Roberts, 1991)
Gruiformes	Otididae	*Tetrax*	*tetrax*	AF	Display	(Veprintsev, 2007)	(Peterson et al., 2001; Roberts, 1991)
Ptercolidiformes	Pteroclididae	*Syrrhaptes*	*paradoxus*	AF	Flight		(Alderfer, 2009)
Columbiformes	Columbidae	*Columba*	*eversmanni*	AF	Flight	XC29188	
Columbiformes	Columbidae	*Columba*	*guinea*	AF	Flight	ML3886	

Columbiformes	Columbidae	*Columba*	*lavata*	AF	Flight	(Gibbon, 2003)	
Columbiformes	Columbidae	*Columba*	*mayeri*	AF, S/C	Flight	ML72182	
Columbiformes	Columbidae	*Columba*	*oenas*	AF	Flight	XC42549	
Columbiformes	Columbidae	*Columba*	*palumbus*	AF, S/C, RU	Flight, Display	XC26550	(Manson-Bahr and Pye, 1985)
Columbiformes	Columbidae	*Columbigallina*	*passerina*	AF, RU?	Flight	(Oberle, 2008)	(Johnston, 1960; Johnston, 1961)
Columbiformes	Columbidae	*Columbina*	*cruziana*	AF, S/C	Flight	(Coopmans et al., 2004)	
Columbiformes	Columbidae	*Drepanoptila*	*holosericea*	AF	Flight		(Baptista et al., 1997; Goodwin, 1983)
Columbiformes	Columbidae	*Ducula*	*bicolor*	AF	Flight	BLOWS: BL W1CDR0000984 BD34	
Columbiformes	Columbidae	*Geotrygon*	*chiriquensis*	AF	Flight		(Baptista et al., 1997; Howell and Webb, 1995)
Columbiformes	Columbidae	*Geotrygon*	*linearis*	AF	Flight	ML64327	
Columbiformes	Columbidae	*Geotrygon*	*veraguensis*	AF	Flight		(Baptista et al., 1997)
Columbiformes	Columbidae	*Goura*	*victoria*	AF, S/C	Flight	XC40937	Baptista et al., 1997)
Columbiformes	Columbidae	*Leptotila*	*jamaicensis*	AF	Flight	CJC unpubl. recording	
Columbiformes	Columbidae	*Leptotila*	*verreauxi*	AF, S/C	Flight	XC2204, ML 64196	
Columbiformes	Columbidae	*Metriopelia*	*aymara*	AF	Flight	XC2468	(Goodwin, 1983)
Columbiformes	Columbidae	*Metriopelia*	*ceciliae*	AF	Flight	XC18380	
Columbiformes	Columbidae	*Metriopelia*	*melanoptera*	AF	Flight	(Krabbe et al., 2001)	
Columbiformes	Columbidae	*Metriopelia*	*morenoi*	AF	Flight	XC32216	
Columbiformes	Columbidae	*Nesoenas*	*mayeri*	AF	Flight		Baptista et al., 1997
Columbiformes	Columbidae	*Ocyphaps*	*lophotes*	AF	Flight; Alarm	(Hingee and Magrath, 2009)	(Hingee and Magrath, 2009)
Columbiformes	Columbidae	*Patagioenas*	*fasciata albilinea*	S/C	Flight	(Jahn et al., 2003)	
Columbiformes	Columbidae	*Phaps*	*histrionica*	AF	Flight		Baptista et al., 1997)

Journal of Experimental Biology • Supplementary information

Columbiformes	Columbidae	*Ptilinopus*	*dupetithouarsii*	AF	Flight		Baptista et al., 1997)
Columbiformes	Columbidae	*Ptilinopus*	*melanospila*	UNCLEAR	Flight		Baptista et al., 1997)
Columbiformes	Columbidae	*Ptilinopus*	*regina*	AF	Flight		Baptista et al., 1997)
Columbiformes	Columbidae	*Ptilinopus*	*superbus*	AF	Flight		Baptista et al., 1997)
Columbiformes	Columbidae	*Scardafella*	*inca*	UNCLEAR	Flight		(Howell and Webb, 1995; Johnston, 1960)
Columbiformes	Columbidae	*Scardafella*	*squammata*	UNCLEAR	Flight		(Sick, 1993)
Columbiformes	Columbidae	*Streptopelia*	*decaocto*	AF, S/C	Flight, Display	CJC unpubl. recording	
Columbiformes	Columbidae	*Treron*	*apicauda*	AF	Flight		Baptista et al., 1997
Columbiformes	Columbidae	*Treron*	*calva*	AF	Flight	ML 4058	
Columbiformes	Columbidae	*Treron*	*phoenicopterus*	AF	Flight	ML 56457	(Goodwin, 1983)
Columbiformes	Columbidae	*Treron*	*pompadora*	S/C	Flight	ML 111553	
Columbiformes	Columbidae	*Treron*	*sphenura*	AF	Flight		(Baptista et al., 1997)
Columbiformes	Columbidae	*Treron*	*vernans*	S/C	Flight	ML 113715	
Columbiformes	Columbidae	*Zenaida*	*asiatica*	AF, S/C	Flight	ML 4037	
Columbiformes	Columbidae	*Zenaida*	*auriculata*	AF	Flight	ESM this study	
Columbiformes	Columbidae	*Zenaida*	*macroura*	AF*	Flight	BL 3243	(Coleman, 2008)
Columbiformes	Columbidae	*Zenaida*	*meloda*	AF, S/C	Flight	(Coopmans et al., 2004)	
Psittaciformes	Psittacidae	*Leptosittata*	*branickii*	AF	Flight	XC 40514	
Psittaciformes	Psittacidae	*Pionites*	*melanocephala*	AF	Flight	XC 9225	
Psittaciformes	Psittaculidae	*Neopsephotus*	*bourkii*	AF	Flight		Goodwin, 1983
Strigiformes	Strigidae	*Asio*	*flammeus*	S/C	Display	ML 137520	(Wiggins et al., 2006)
Strigiformes	Strigidae	*Asio*	*otus*	S/C	Display	ML 48903	(Marks et al., 1994)
Strigiformes	Strigidae	*Glaucidium*	*gnoma*	AF	Flight		(Holt and Petersen, 2000)
Strigiformes	Strigidae	*Strix*	*varia*	S/C	Display		(Whiklo and Duncan, 2012)
Strigiformes	Tytonidae	*Tyto*	*alba*	S/C	Display		(Marti et al., 2005))
Caprimulgiformes	Caprimulgidae	*Eleothreptus*	*candicans*	IA	Display	XC 15334	(Cleere and Nurney, 1998)

Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*carolinensis*	S/C	Display		(Mengel, 1972)
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*cayennensis*	AF	Display	ML 60664, ML 74675	(Cleere and Nurney, 1998)
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*europaeus*	S/C	Display	XC 25587	(Manson-Bahr and Pye, 1985; Mengel, 1972)
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*longirostris*	AF?, S/C	Display	(Krabbe and Nilsson, 2003)	
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*maculicaudus*	AF, S/C	Flight, Display	(Ranft and Cleere, 2000)	(Cleere and Nurney, 1998; Sick, 1993)
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*ruficollis*	S/C	Display	(Ranft and Cleere, 2000)	
Caprimulgiformes	Caprimulgidae	*Chordeiles*	*gundlachii*	AF	Display		(Cleere and Nurney, 1998)
Caprimulgiformes	Caprimulgidae	*Chordeiles*	*minor*	AF	Display	XC 7700	(Manson-Bahr and Pye, 1985; Miller, 1925)
Caprimulgiformes	Caprimulgidae	*Eleothreptus*	*anomalus*	WW	Display	(Ranft and Cleere, 2000)	(Cleere and Nurney, 1998; Sick, 1993)
Caprimulgiformes	Caprimulgidae	*Eurostopodus*	*mystacalis*	AF	Display		(Cleere and Nurney, 1998)
Caprimulgiformes	Caprimulgidae	*Hydropsalis*	*brasiliana*	S/C	Display		Sick, 1993
Caprimulgiformes	Caprimulgidae	*Hydropsalis*	*climacocerca climacocerca*	AF	Display	(Moore et al., 2009)	
Caprimulgiformes	Caprimulgidae	*Macrodipteryx*	*longipennis*	UNCLEAR	Display		(Cleere and Nurney, 1998)
Caprimulgiformes	Caprimulgidae	*Phalaenoptilus*	*nutallii*	S/C	Display		(Mengel, 1972)
Apodiformes	Apodidae	*Chaetura*	*spinicaudus*	S/C	Flight	(Renaudier and Deroussen, 2008)	
Apodiformes	Apodidae	*Cypseloides*	*senex*	AF	Flight	XC 15429	

Journal of Experimental Biology • Supplementary information

Apodiformes	Trochilidae	*Campylopterus*	*sp*	S/C	Display		Sick, 1993
Apodiformes	Trochilidae	*Coeligena*	*bonapartei*	S/C	Agonistic	CJC pers. obvs	
Apodiformes	Trochilidae	*Lesbia*	*victoriae*	S/C	Display	ESM this study	(Ortiz-Crespo, 2003)
Apodiformes	Trochilidae	*Lophornis*	*magnifica*	AF	Display		(Sick, 1993)
Apodiformes	Trochilidae	*Ocreatus*	*underwoodii*	S/C	Display	ESM this study	
Apodiformes	Trochilidae	*clade Mellisuginae*	*~38 spp in various genera*	AF*, WW, S/C	Flight, Display	see refs	(Clark, 2011; Clark et al., 2011a; Clark and Feo, 2008; Clark and Feo, 2010; Clark et al., 2011b; Feo and Clark, 2010; Hunter, 2008; Hunter and Picman, 2005; Miller and Inouye, 1983)
Apodiformes	Trochilidae	*Phaethornis*	*ruber*	UNCLEAR	Display		(Sick, 1993)
Apodiformes	Trochilidae	*Popelairia*	*sp*	AF?	Display	ESM this study	Sick, 1993
Apodiformes	Trochilidae	*Trochilus*	*sp*	AF*	Flight, Display	(Clark, 2008)	(Clark, 2008)
Coraciiformes	Brachypteraciidae	*Uratelornis*	*chimaera*	S/C	Display	(Hawkins and Ranft, 2007)	(Tobias and Seddon, 2003)
Bucerotiformes	Bucerotidae	*Aceros*	*cassidix*	AF	Flight	BLOWS: BL W1CDR0000458 BD17	
Bucerotiformes	Bucerotidae	*Aceros*	*comatus*	AF	Flight	XC19131	
Bucerotiformes	Bucerotidae	*Aceros*	*corrugatus*	AF	Flight	XC21026	(Kemp, 1995)
Bucerotiformes	Bucerotidae	*Aceros*	*nipalensis*	AF, RU	Flight	BLOWS: BL W ACEROS NIPALENSIS R1 C4	
Bucerotiformes	Bucerotidae	*Aceros*	*undulatus*	AF	Flight	BLOWS: BL 022A-WA01035X0005-	Kemp 1995

						0005M0.WAV	
Bucerotiformes	Bucerotidae	*Buceros*	*rhinoceros*	AF	Flight		(Kemp, 1995; Manson-Bahr and Pye, 1985)
Bucerotiformes	Bucerotidae	*Bycanistes*	*subcylindricus*	AF	Flight	ESM this study	
Bucerotiformes	Bucerotidae	*Ceratogymna*	*atrata*	AF	Flight	ML87146	
Bucerotiformes	Bucerotidae	*Ceratogymna*	*brevis*	AF	Flight		Kemp, 1995
Bucerotiformes	Bucerotidae	*Ceratogymna*	*cylindricus*	AF	Flight		Kemp, 1995
Bucerotiformes	Bucerotidae	*Ceratogymna*	*elata*	AF	Flight		Kemp, 1995
Bucerotiformes	Bucerotidae	*Ocyceros*	*birostris*	AF	Flight		(Kemp, 1995; Roberts, 1991)
Bucerotiformes	Bucerotidae	*Penelopides*	*panini*	AF	Flight		Kemp, 1995
Bucerotiformes	Bucerotidae	*Rhinoplax*	*vigil*	AF	Flight	BLOWS: BLW RHINOPLAX VIGIL R1 C5	
Coraciiformes	Todidae	*Todus*	*angustirostris*	WW	Display		(Kepler, 1977; Raffaele et al., 1998)
Coraciiformes	Todidae	*Todus*	*mexicanus*	WW*	Display	ML129711	(Kepler, 1977; Raffaele et al., 1998)
Coraciiformes	Todidae	*Todus*	*multicolor*	WW	Display	ML113260; ESM of this study	(Kepler, 1977; Manson-Bahr and Pye, 1985; Raffaele et al., 1998)
Coraciiformes	Todidae	*Todus*	*subulatus*	WW	Display	ML6613	(Kepler, 1977; Raffaele et al., 1998)
Piciformes	Bucconidae	*Notharchus*	*macrorhynchos*	UNCLEAR	Flight		(Howell and Webb, 1995)
Piciformes	Bucconidae	*Notharchus*	*ordii*	RU	Flight	ML89121	
Piciformes	Indicatoridae	*Indicator*	*indicator*	RU, WW	Display	ML37839	(Friedmann, 1955)
Piciformes	Indicatoridae	*Indicator*	*minor*	RU	Display	ML58531	Friedmann, 1955
Piciformes	Indicatoridae	*Melichneutes*	*robustus*	AF*	Display	BLOWS:	(Friedmann, 1955; Manson-

						BLW1CDR0000051 BD4	Bahr and Pye, 1985)
Piciformes	Picidae	*Canpephilus*	*leucopogon*	AF	Flight	XC29092	
Piciformes	Picidae	*Dryocopus*	*martinus*	AF	Flight	XC41719	
Piciformes	Ramphastidae	*Aulacorhynchus*	*prasinus*	RU	Flight	ML65034	(Howell and Webb, 1995; Stiles and Skutch, 1989)
Piciformes	Ramphastidae	*Ramphastos*	*sulfuratus*	UNCLEAR	Flight		(Howell and Webb, 1995)
Piciformes	Ramphastidae	*Ramphastos*	*tucanus*	RU	Flight	ML113119	
Trogoniformes	Trogonidae	*sp*		AF	Flight	CJC pers. obvs	
Passeriformes	Alaudidae	*Mirafra*	*apiata*	S/C	Display	BLOWS: BL 022A-WA09006X0001-0021M0.WAV	(Manson-Bahr and Pye, 1985; Ryan and Marshall, 2005)
Passeriformes	Alaudidae	*Mirafra*	*hypermetra*	S/C	Display	ML102159	
Passeriformes	Alaudidae	*Mirafra*	*rufocinnamomea*	S/C	Display	ML8043	(Bertram, 1977; Norberg, 1991; Payne, 1973)
Passeriformes	Cisticolidae	*Apalis*	*binotata*	S/C	Display	CJC recording	
Passeriformes	Cisticolidae	*Apalis*	*flavida*	S/C	Display	ML80027	
Passeriformes	Cisticolidae	*Apalis*	*melanocephala*	S/C	Display	ML49863	
Passeriformes	Cisticolidae	*Apalis*	*nigriceps*	S/C	Display	ML86969	
Passeriformes	Cisticolidae	*Apalis*	*rufogularis*	S/C	Display	ML107812	
Passeriformes	Cisticolidae	*Apalis*	*thoracica*	S/C	Display	XC29275	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Calamonastes*	*fasciolatus*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*aridulus*	S/C	Display	(Gibbon, 2003)	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*ayresii*	S/C	Display	ML14358	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*brunnescens*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*cherina*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*chubbi*	S/C	Display	ML49642	(Ryan et al., 2006)

Passeriformes	Cisticolidae	*Cisticola*	*dambo*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*erythrops*	S/C	Display	ML14380	
Passeriformes	Cisticolidae	*Cisticola*	*eximius*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*fulvicapilla*	S/C	Display	ML69161	
Passeriformes	Cisticolidae	*Cisticola*	*galactotes*	WW	Display	ML100328	
Passeriformes	Cisticolidae	*Cisticola*	*hunteri*	WW	Display	ML14396	
Passeriformes	Cisticolidae	*Cisticola*	*juncidis*	RU	Display	ML104926	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*lateralis*	S/C	Display	ML87395	
Passeriformes	Cisticolidae	*Cisticola*	*melanurus*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*nigriloris*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*njombe*	S/C	Display	ML49640	
Passeriformes	Cisticolidae	*Cisticola*	*pipiens*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*rufilatus*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Cisticola*	*textrix*	S/C	Display	ML80625	
Passeriformes	Cisticolidae	*Cisticola*	*tinniens*	AF	Display	ML14516	
Passeriformes	Cisticolidae	*Prinia*	*cinereocapilla*	S/C	Display	ML111508	
Passeriformes	Cisticolidae	*Prinia*	*flaviventris*	S/C	Display	ML113733	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Prinia*	*inornata*	S/C	Display	ML11567	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Prinia*	*molleri*	S/C	Display	ML96219	(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Prinia*	*socialis*	S/C	Display		(Ryan et al., 2006)
Passeriformes	Cisticolidae	*Prinia*	*subflava*	S/C	Display	ML14561	
Passeriformes	Conopophagidae	*Conopophaga*	*ardesiaca*	WW	Display	XC3579	
Passeriformes	Conopophagidae	*Conopophaga*	*aurita*	WW	Display	ML126817	
Passeriformes	Conopophagidae	*Conopophaga*	*castaneiceps*	WW	Display	ML92822	
Passeriformes	Conopophagidae	*Conopophaga*	*lineata*	WW	Display	XC39993	(Sick, 1965; Sick, 1993)
Passeriformes	Conopophagidae	*Conopophaga*	*melanops*	WW	Display	ML127982	
Passeriformes	Corvidae	*Aphelocoma*	*wollweberi*	AF	Flight	CJC recording	

Passeriformes	Corvidae	*Corvus*	*corax*	AF	Flight	Mark Brennan pers. comm.	
Passeriformes	Cotingidae	*Ampelion*	*rubrocristata*	WW	Display	ML21940	
Passeriformes	Cotingidae	*Capornis*	*cucullatus*	RU	Flight	ML112751	
Passeriformes	Cotingidae	*Cephalopterus*	*penduliger*	S/C	Display	XC15096	
Passeriformes	Cotingidae	*Chirocylla*	*uropygialis*	UNCLEAR	?		(Snow, 1982)
Passeriformes	Cotingidae	*Cotinga*	*cayana*	WW	Display	(Krabbe and Nilsson, 2003)	
Passeriformes	Cotingidae	*Cotinga*	*cotinga*	S/C*	Display	César Sánchez pers. comm.	(Sick, 1993; Snow, 1982)
Passeriformes	Cotingidae	*Cotinga*	*maculata*	AF	Display		(Sick, 1993)
Passeriformes	Cotingidae	*Cotinga*	*maynana*	AF	Display	César Sánchez pers. comm.	
Passeriformes	Cotingidae	*Cotinga*	*nattererii*	AF	Display	César Sánchez pers. comm.	
Passeriformes	Cotingidae	*Cotinga*	*ridgwayi*	AF	Display	César Sánchez pers. comm.	
Passeriformes	Cotingidae	*Laniisoma*	*elegans*	UNCLEAR	Display		(Snow, 1982)
Passeriformes	Cotingidae	*Lipaugus*	*lanioides*	UNCLEAR	?		(Snow, 1982)
Passeriformes	Cotingidae	*Phoenicircus*	*carnifex*	AF	Display	ML115234	(Snow, 1982; Trail and Donahue, 1991)
Passeriformes	Cotingidae	*Phoenicircus*	*nigricollis*	AF	Display	ML148734	(Trail and Donahue, 1991)
Passeriformes	Cotingidae	*Pipreola*	*riefferii occidentalis*	AF	Flight	(Jahn et al., 2003)	
Passeriformes	Cotingidae	*Rupicola*	*peruvianus*	AF	Flight	ML120891	
Passeriformes	Cotingidae	*Rupicola*	*ripicola*	RU	Flight		(Sick, 1993; Snow, 1982)

Passeriformes	Cotingidae	*Xipholena*	*atropurpurea*	RU	Display		(Sick, 1993)
Passeriformes	Cotingidae	*Zaratornis*	*stresemanni*	RU	Display	ML11079	
Passeriformes	Drepaniidae	*Himatione*	*sanguinea*	WW*	Display	ML5143	(Amadon, 1950)
Passeriformes	Drepaniidae	*Vestiaria*	*coccinea*	WW	Display	ML6034	Amadon, 1950
Passeriformes	Emberizidae	*Amphispiza*	*bilineata*	WW	Display	XC111321	de Queiroz pers. comm.
Passeriformes	Eurylaimidae	*Pseudocalyptomena*	*graueri*	AF	Flight		(Lambert and Woodcock, 1996)
Passeriformes	Eurylaimidae	*Smithornis*	*capensis*	AF*	Display	ML80390	(Lambert and Woodcock, 1996)
Passeriformes	Eurylaimidae	*Smithornis*	*rufolateralis*	AF*	Display	ML87130	(Lambert and Woodcock, 1996)
Passeriformes	Eurylaimidae	*Smithornis*	*sharpei*	AF	Display	BLOWS: BLW SMITHORNIS SHARPEI R1 C1	(Lambert and Woodcock, 1996)
Passeriformes	Furnarinidae	*Cinclodes*	*fuscus*	AF	Display	XC89742	
Passeriformes	Icteridae	*Icterus*	*cucullatus*	AF	Flight	XC21403	
Passeriformes	Icteridae	*Psarocolius*	*montezuma*	S/C	Display	ML89453	M. Webster pers. comm.
Passeriformes	Icteridae	*Psarocolius*	*wagleri*	RU	Flight, Display	(Jahn et al., 2003)	(Chapman, 1928; Howell and Webb, 1995)
Passeriformes	Meliphagidae	*Anthornis*	*melanura*	AF	Flight, Display	ML136132	(Craig, 1984; Craig, 1985)
Passeriformes	Meliphagidae	*Prosthemadera*	*novaeseelandiae*	AF*	Flight, Display	ML136117	Craig 1984
Passeriformes	Paradisaeidae	*Astrapia*	*mayeri*	RU	Flight	ML107097	(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Astrapia*	*rothschildi*	AF	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Astrapia*	*splendidissima*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Astrapia*	*stephaniae*	RU	Display		(Frith and Beehler, 1998; Manson-Bahr and Pye, 1985)
Passeriformes	Paradisaeidae	*Cicinnurus*	*magnificus*	UNCLEAR	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Cicinnurus*	*regius*	UNCLEAR	Display		(Frith and Beehler, 1998)

Passeriformes	Paradisaeidae	*Cicinnurus*	*respublica*	S/C	Display	XC23182	(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Cnemophilus*	*macgregorii*	UNCLEAR	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Epimachus*	*meyeri*	S/C	Display		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Lophorina*	*superba*	RU	Flight	ML 458003	(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Lycocorax*	*pyrrhopterus*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Macgregoria*	*pulchra*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Manucodia*	*atra*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Manucodia*	*chalybata*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Manucodia*	*comrii*	UNCLEAR	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Paradigalla*	*brevicauda*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Paradisaea*	*raggiana*	UNCLEAR	Display		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Paradisaea*	*rubra*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Parotia*	*carolae*	S/C	Flight, Display		(Frith and Beehler, 1998; Scholes, 2006)
Passeriformes	Paradisaeidae	*Parotia*	*sefilata*	RU	Display	XC40930	
Passeriformes	Paradisaeidae	*Parotia*	*wahnesi*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Ptiloris*	*magnificus*	AF, S/C, RU	Flight, Display	BLOWS: BL Magnificent Rifle-bird.wav, ML 455444	(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Ptiloris*	*paradiseus*	UNCLEAR	Display		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Ptiloris*	*victoriae*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Seleucidis*	*melanoleuca*	RU	Flight		(Frith and Beehler, 1998)
Passeriformes	Paradisaeidae	*Semioptera*	*wallacii*	?	Flight		(Frith and Beehler, 1998)
Passeriformes	Philepittidae	*Neodrepanis*	*coruscans*	AF	Flight	ML97926	(Lambert and Woodcock, 1996)
Passeriformes	Philepittidae	*Neodrepanis*	*hypoxantha*	AF	Flight		(Lambert and Woodcock, 1996)
Passeriformes	Phyloscopidae	*Phylloscopus*	*borialis*	S/C	Display	Chris Benesh pers. comm.	(Lowther and Sharbaugh, 2008)

Passeriformes	Pipridae	*Corapipo*	*gutturalis*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Corapipo*	*heteroleuca*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Corapipo*	*altera*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Chiroxiphia*	*caudata*	S/C	Display	ML 142254?, IBC	
Passeriformes	Pipridae	*Chiroxiphia*	*lanceolata*	S/C, MISC	Display	(DuVal, 2007)	(DuVal, 2007)
Passeriformes	Pipridae	*Ilicura*	*militaris*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Heterocercus*	*aurantiivertex*	UNCLEAR	Display		(Alonso, 2000; Prum, 1998)
Passeriformes	Pipridae	*Heterocercus*	*flavivertex*	AF	Display		(Prum, 1998)
Passeriformes	Pipridae	*Heterocercus*	*lineatus*	AF	Display	Richard Hoyer pers. comm.	(Prum, 1998)
Passeriformes	Pipridae	*Machaeropterus*	*pyrocephalus*	S/C	Display	(Marantz and Zimmer, 2007)	
Passeriformes	Pipridae	*Machaeropterus*	*deliciosus*	MISC	Display		(Bostwick and Prum, 2005)
Passeriformes	Pipridae	*Manacus*	*aurantiacus*	S/C, WW	Display	ML 28214	(Bostwick and Prum, 2003)
Passeriformes	Pipridae	*Manacus*	*candei*	S/C	Display	ML 72655	
Passeriformes	Pipridae	*Manacus*	*manacus*	S/C, WW, RU	Display	ML 38860	(Bostwick and Prum, 2003)
Passeriformes	Pipridae	*Manacus*	*vitellinus*	S,C, WW	Display	ML 37784	
Passeriformes	Pipridae	*Pipra*	*aureola*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Pipra*	*erythrocephala*	S/C	Display	ML 7313	
Passeriformes	Pipridae	*Pipra*	*fasciicauda*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Pipra*	*filicauda*	S/C, MISC	Display		Prum 1998
Passeriformes	Pipridae	*Pipra*	*cornuta*	S/C	Display		Prum 1998
Passeriformes	Pipridae	*Pipra*	*iris*	WW	Display	ML 115231	
Passeriformes	Pipridae	*Pipra*	*mentalis*	S/C, MISC	Display		(Bostwick and Prum, 2003)
Passeriformes	Pipridae	*Pipra*	*chloromeros*	S/C	Display		Prum 1998

Passeriformes	Pittidae	*Pitta*	*angolensis*	AF	Display	BLOWS: BL W PITTA ANGOLENSIS R1 C11	(Chapin, 1953)
Passeriformes	Pittidae	*Pitta*	*reichenowi*	?	Display		(Chapin, 1953)
Passeriformes	Pittidae	*Pitta*	*ussheri*	WW	Display	ML 169902	(Pegan et al., 2013)
Passeriformes	Promeropidae	*Promerops*	*cafer*	S/C	Display		(Calf et al., 2003)
Passeriformes	Promeropidae	*Promerops*	*gurneyi*	S/C	Display		(Calf et al., 2001)
Passeriformes	Sturnidae	*Lamprocolius*	*chalybaeus*	UNCLEAR	Flight		(Vincent, 1936)
Passeriformes	Sturnidae	*Onychognathus*	*morio*	UNCLEAR	Flight		Wilson Nderitu pers. comm.
Passeriformes	Thraupidae	*Volatinia*	*jacarina*	S/C	Display	ML 165048	(Fandiño-Mariño and Vielliard, 2004)
Passeriformes	Tityridae	*Pachyramphus*	*castaneus*	S/C	?		(Sick, 1993)
Passeriformes	Tityridae	*Pachyramphus*	*cinnamomeus*	S/C	Display	ML 28106	
Passeriformes	Tityridae	*Pachyramphus*	*major*	WW	Flight	ML 103322	
Passeriformes	Tityridae	*Pachyramphus*	*marginatus*	WW	Flight	ML 112255	
Passeriformes	Tityridae	*Pachyramphus*	*minor*	RU	Flight	(Marantz and Zimmer, 2007)	
Passeriformes	Tityridae	*Pachyramphus*	*niger*	RU	Flight	ML 56169	
Passeriformes	Tityridae	*Pachyramphus*	*viridis*	UNCLEAR	Display		(Sick, 1993)
Passeriformes	Tityridae	*Tityra*	*semifasciata*	WW	Flight	ML 62800	(Sick, 1993)
Passeriformes	Tityridae	*Tityra*	*cayana*	AF	Display	ML 30838	

Passeriformes	Tyrannidae	*Alectrurus*	*risora*	WW	Display	ML 132886	
Passeriformes	Tyrannidae	*Alectrurus*	*tricolor*	UNCLEAR	Display		(Fitzpatrick, 2004; Sick, 1993)
Passeriformes	Tyrannidae	*Arundinicola*	*leucocephala*	S/C, WW	Flight	ML 51840	(Sick, 1993)
Passeriformes	Tyrannidae	*Atalotriccus*	*pilaris*	S/C	Display	ML 28301	Fitzpatrick 2004
Passeriformes	Tyrannidae	*Cnipodectes*	*subbrunneus*	AF	Display	ML 148751	
Passeriformes	Tyrannidae	*Cnipodectes*	*superrufus*	AF	Display	XC 40219	(Lane et al., 2007)
Passeriformes	Tyrannidae	*Griseotyrannus*	*aurantioatrocristatus*	RU	?		(Sick, 1993)
Passeriformes	Tyrannidae	*Hemitriccus*	*granadensis*	AF	Display	(Krabbe et al., 2001)	
Passeriformes	Tyrannidae	*Hemitriccus*	*mirandae*	AF	Display	XC 4990	
Passeriformes	Tyrannidae	*Hemitriccus*	*orbitatus*	AF	Display	XC 33241	
Passeriformes	Tyrannidae	*Hymenops*	*perspicillatus*	AF	Flight, Display	ML 132640	(Fitzpatrick, 2004; Sick, 1993)
Passeriformes	Tyrannidae	*Knipolegus*	*aterrimus*	S/C	Display	BLOWS: BL022A-WA07021XXXXX-0614M0.WAV	
Passeriformes	Tyrannidae	*Knipolegus*	*hudsoni*	UNCLEAR	?		Fitzpatrick, 2004
Passeriformes	Tyrannidae	*Knipolegus*	*orenocensis*	S/C	Display	ML 45574	
Passeriformes	Tyrannidae	*Knipolegus*	*peocilocercus*	UNCLEAR	?		Sick, 1993
Passeriformes	Tyrannidae	*Knipolegus*	*poecilurus*	S/C	Display	XC 36084	
Passeriformes	Tyrannidae	*Knipolegus*	*signatus*	WW	Flight	XC 29356	
Passeriformes	Tyrannidae	*Knipolegus*	*striaticeps*	UNCLEAR	?		Fitzpatrick ,2004
Passeriformes	Tyrannidae	*Lessonia*	*oreas*	AF	Display	ML 171116	(Areta and Miller, 2014)
Passeriformes	Tyrannidae	*Lipaugus*	*fuscorinereus*	AF	Display	XC 45250	(López-Lanús, 2000)
Passeriformes	Tyrannidae	*Mecocerculus*	*leucophrys setophagoides*	AF	?	(Alvarez et al., 2007)	
Passeriformes	Tyrannidae	*Mionectes*	*macconnelli*	RU, WW	Flight	ML 127787	
Passeriformes	Tyrannidae	*Mionectes*	*oleagineus*	WW	Display	ML 115765	

Passeriformes	Tyrannidae	*Mionectes*	*rufiventris*	RU, WW	Flight	ML 39089	Fitzpatrick, 2004
Passeriformes	Tyrannidae	*Musciasaxicola*	*maculirostris maculirostris*	S/C	Display	(Alvarez et al., 2007)	
Passeriformes	Tyrannidae	*Myiozetetes*	*cayanensis hellmayri*	AF	Display	(Jahn et al., 2003)	
Passeriformes	Tyrannidae	*Neoxolmis*	*rubetra*	WW?	Display		Wetmore 1926, in Areta and Miller, 2014
Passeriformes	Tyrannidae	*Phylloscartes*	*beckeri*	AF	Display	XC 6289	
Passeriformes	Tyrannidae	*Phylloscartes*	*ventralis*	WW	Display	(Gonzaga and Castiglioni, 2001)	
Passeriformes	Tyrannidae	*Pipromorpha*	*oleaginea*	UNCLEAR	?		(Snow and Snow, 1979)
Passeriformes	Tyrannidae	*Platyrinchus*	*coronatus*	AF	Flight	ML134869	(Stiles and Skutch, 1989)
Passeriformes	Tyrannidae	*Platyrinchus*	*mystaceus*	AF	?	ML135697	
Passeriformes	Tyrannidae	*Polystictus*	*pectoralis*	?			(Areta and Miller, 2014)
Passeriformes	Tyrannidae	*Poecilotriccus*	*ruficeps*	S/C	Display	XC11046	
Passeriformes	Tyrannidae	*Pseduocolopteryx*	*sclateri*	UNCLEAR	Display		(Bostwick and Zyskowski, 2001; Sick, 1993)
Passeriformes	Tyrannidae	*Pseudocolopteryx*	*acutipennis*	AF, WW	Display	(Krabbe et al., 2001)	
Passeriformes	Tyrannidae	*Pseudotriccus*	*pelzelni*	S/C	Display	XC 12894	
Passeriformes	Tyrannidae	*Pseudotriccus*	*ruficeps*	S/C	Display	(Krabbe et al., 2001)	
Passeriformes	Tyrannidae	*Pseudotriccus*	*simplex*	S/C	Display	XC 3422	
Passeriformes	Tyrannidae	*Pyrocephalus*	*rubinus*	WW*	Display	ESM of this study	(Smith, 1967)
Passeriformes	Tyrannidae	*Todirostrum*	*cinereum*	S/C	?	(Coopmans et al., 2004)	
Passeriformes	Tyrannidae	*Tyrannus*	*albogularis*	UNCLEAR	Flight		Sick, 1993

Passeriformes	Tyrannidae	*Tyrannus*	*couchii*	WW	Flight, Display	ML112690	(Smith, 1966)
Passeriformes	Tyrannidae	*Tyrannus*	*cubensis*	AF	Display	ML62959	
Passeriformes	Tyrannidae	*Tyrannus*	*dominicensis*	WW	Display	ML53841	(Post, 1982; Smith and Jackson, 2002)
Passeriformes	Tyrannidae	*Tyrannus*	*forficatus*	AF*	Display	ML45053	(Regosin, 1998; Smith, 1966)
Passeriformes	Tyrannidae	*Tyrannus*	*melancholicus*	WW	Flight	ML59884	(Stiles and Skutch, 1989; Stouffer and Chesser, 1998)
Passeriformes	Tyrannidae	*Tyrannus*	*savana*	UNCLEAR	Display		(Sick, 1993; Stiles and Skutch, 1989)
Passeriformes	Tyrannidae	*Tyrannus*	*tyrannus*	WW	Display	BLOWS: BLW1CDR0000689 BD2	(Murphy, 1996; Smith, 1966)
Passeriformes	Tyrannidae	*Tyrannus*	*verticalis*	WW	Display	XC 12126	(Gamble and Bergin, 2012; Smith, 1966)
Passeriformes	Tyrannidae	*Tyrannus*	*vociferans*	WW	Display		(Smith, 1966; Tweit and Tweit, 2000)
Passeriformes	Tyrannidae	*Xolmis*	*dominicanus*	UNCLEAR	?		Fitzpatrick, 2004
Passeriformes	Tyrannidae	*Xolmis*	*irupero*	UNCLEAR	?		Sick, 1993
Passeriformes	Tyrannidae	*Xolmis*	*salinarum*	AF	Flight	XC 8991	

[1] **AF**: aeroelastic flutter (includes apparent flutter-induced feather collisions); **WW**: wing whirring; **S/C**: snap or clap (percussion); **RU**: rustling; **MISC**: other mechanisms (see text), **UNCLEAR**: written description of sound does not provide adequate clues as to the type or mechanism of sound. * indicates feathers tested in wind tunnel in this study (non-hummingbirds) or prior study (hummingbirds).

[2] **Flight** = ordinary flight, seemingly not modulated. **Agonistic** = aggressive interactions apparently by both sexes and not in the context of breeding; **Alarm** = functions as an alarm signal (Hingee and Magrath 2009). **Display** = any sort of sexual function in which

it is produced by primarily or exclusively one sex. This includes courtship displays (i.e. male displays directed at a female), song-equivalent (undirected sound broadcast into the environment), and male-male agonistic interactions in the context of a breeding territory.

[3] Citations are commercial CDs, computer software, or papers that present a spectrogram. Abbreviations: **BLOWS**: British Library of Wildlife Sounds; **ML**: Macaulay Library of Natural Sound http://macaulaylibrary.org/; **XC**: xeno-canto http://www.xeno-canto.org/

This table was complied by searching the literature for instances in which authors mention any sort of nonvocal sound produced by the wings or tail, either during flight or in a display (including perched displays), as well as taxa that came up in our searches of sound recording databases (in 2010), and our own field observations. Whooshes are not included, as these sounds are the inevitable result of turbulence and are therefore produced by all flying birds, nor are humming sounds, which are inevitably produced by birds with an wingbeat frequency audible to humans (humming of hummingbirds). This table is not exhaustive and we presumably missed relevant references or recordings for additional taxa.

Some sonations are produced in place of vocal song, i.e. they serve as a general territorial advertisement and seem to serve male-male competition as well as female choice. Other sonations are produced during specific, targeted displays by males for females. A couple may be produced primarily by males for other males in the context of aggressive interactions and competition for a breeding territory. Despite the large differences in these ecological contexts, all of these types of sounds are lumped under ‘display’, as many references did not provide more detailed information to discern more specific contexts in which the sonation was produced.

The data in Table S1 are biased. Obviously, there must be more birds that produce some sort of flight sound in ordinary flight that we did not discover. There are also two less obvious biases. First, nonvocal sounds produced during display are not necessarily sonations. The criteria for inclusion in the table was whether a nonvocal sound was mentioned in a natural history reference, particularly in the context of a display. However, authors' descriptions often did not provide enough information to determine which of these sounds may have been salient (rather than incidental or adventitious) during displays. Some authors comment extensively on wing sounds, causing these clades to be well-sampled, whereas others seemed to take them for granted, and therefore failed to mention them (resulting in under-sampling). For instance, Frith & Bheeler (1998) mention the wing sounds of many birds-of-paradise, including sounds produced during courtship displays. These sounds are mostly rustling sounds that, for a bird producing complex motions, may be unavoidable (adventitious). These sounds may not be salient to other birds, or otherwise important components of the display. These sounds are included here with a context of "display". Thus, birds of paradise therefore may be over-represented in Table S1, and are indicated as producing sound during display (as opposed to ordinary flight). We infer two origins of sonations in this clade, because two species in this clade make apparent, loud non-vocal sounds: *Ptiloris magnificus* (see ML 455444; mechanism: rustling) and *Lophorina superba* (see ML 458003; mechanism: snapping). However, the others may *not* produce specialized non-vocal sounds that are the direct target of sexual selection. Rather, sound was produced as an inevitable byproduct of a vigorous display. Thus, taxa reported as producing a sound in display may **not** produce a sonation-- display sounds could be adventitious, not functional.

Second, and related: the inferences of mechanism of sound production come from our assessment of the acoustic form of the sound recording indicated, or from authors' descriptions when a sound recording was unavailable. Rarely, we obtained a recording of a nonvocal sound that did not match the physical mechanism we expected, relative to what closely related taxa do. While this mismatch could be real (closely related taxa have nonetheless evolved differences in physical mechanism), this result could also arise if a species produces both adventitous sounds and sonations, but the only recording available contained an adventitious sound. Thus the recording we scored may not accurately reflect the mechanisms used to produce the most noteworthy or important mechanical sound of a given species. For instance, *Cisticola* spp. produce percussive snapping sonations (Ryan et al., 2006); but the only recording of *Cisticola hunter* that we found that contained non-vocal sounds was ML14396, which included a wing whirr but no snapping. In the table, this species is coded as producing a wing whirr, but this seemed to simply be an incidental byproduct of a song display. This second bias seemed sufficiently rare that we do not think it has affected any of the conclusions in the manuscript.

Journal of Experimental Biology • Supplementary information

Table S2. Results of wind tunnel tests of whether a feather can produce sounds (via flutter) that match a bird's flight sound.

Family	Species	Feathers tested	Hypothesized source	Flight sound (kHz)	Flutter[1] (kHz)	U* (m s^{-1})	Match[2]	criteria failed[3]
Anatidae	Wood Duck *Aix sponsa*	P10, P9	Outer primaries?	1.6	n/a	n/a	No[4]	4
Anatidae	American Wigeon *Anas americana*	P10, P9	Outer primaries?	1	0.7	20.4	No[4]	3, 4
Anatidae	Gadwall *Anas strepera*	P10, P9	Outer primaries?	5.0	n/a	n/a	No[4]	4
Anatidae	Comm.on Goldeneye *Beucephala clangula*	P10	Outer primaries?	1.4	n/a	n/a	No[4]	4
Anatidae	Barrow's Goldeneye *Beucephala islandica*	P10, P9	Outer primaries?	1.2	2.6	22.0	Yes	
Columbidae	White-tipped Dove *Leptotila verreauxi*	P10	Outer primaries?	0.39	6.2	19.6	No[4]	1
Columbidae	Crested Pigeon *Ocyphaps lophotes*	P8 (modified)	P8 (gap)	2.89	3.1	18.8	Yes	
Columbidae	Mourning Dove *Zenaida macroura*	Outer primary	Outer primaries?	1.95	1.2	19.6	Yes	
Todidae	Puerto Rican Tody *Todus mexicanus*	Outer primary[1]	Outer primaries?	1.6	1.5	12.4	No	2?, 4
Indicatorida e	Lyre-tailed Honeyguide *Melechneutes robustus*	R3, R4, R5, R6	Stiffened rectrices, R2- R6	1.3	1.2	18.8	Yes	
Otidae	Lesser Florican *Sphytinoidies indica*	P10	Attenuated outer primaries	2.43	3	13.2	No	4
Otidae	Little Bustard	P7	P7 (gap)	5.3	0.97	14.0	No[4]	1

Journal of Experimental Biology • Supplementary information

	Tetrax tetrax							
Scolopacidae	Wilson's Snipe *Gallinago delicata*	R8, R7 (outer)	Outer rectrices	0.60	0.6	11.6	Yes	
Scolopacidae	Comm.on Snipe *Gallinago gallinago*	Outer Rectrix	Outer rectrices	0.37	0.2	9.2	Yes	
Scolopacidae	Andean Snipe *Gallinago jamesoni*	Outer, 2nd to outer Rectrix	Outer rectrices	0.26	0.9	15.6	Yes	
Scolopacidae	Swinhoe's Snipe *Gallinago megala*	Outer, 2nd to outer Rectrix	Outer rectrices	1.9	1.1	16.4	Yes	
Scolopacidae	Wood Snipe *Gallinago nemoricola*	Outer Rectrix	Outer rectrices	3.5	3.4	20.4	Yes	
Scolopacidae	South American Snipe *Gallinago paraguaiae*	Outer Rectrix	Outer rectrices	0.62	2.2	16.4	Yes	
Scolopacidae	Pin-tailed Snipe *Gallinago stenura*	Outer, 2nd to outer Rectrix	Outer rectrices	4.2	4.1	18.8	Yes	
Scolopacidae	American Woodcock *Scolopax minor*	P9 (2), P8 (2), P7 (2)	P7, P8, P9	4.5	5.1	16.4	Yes	
Conopopha-gidae	Rufous Gnateater *Conopophaga lineata*	P6, P7, P8, P9	P6 – P9	0.6	1.2	13	No	3, 4
Cotingidae	Red-crested Cotinga *Ampelion rubrocristata*	P10	Outer primaries?	2.7	n/a	n/a	No	4
Cotingidae	Purple-breasted Cotinga *Cotinga cotinga*	P10	Outer primaries?	4.5	3.5	13	No	1, 4
Cotingidae	Guianan Red-Cotinga *Phoenicercus carnifex*	P8	P8 (gap with neighbors)	4	6.7	22.1	No[4]	1 - 4
Cotingidae	Black-necked Red-Cotinga	P8	P8 (gap with neighbors)	5	n/a	n/a	No[4]	4

	Phoenicercus nigricollis							
Tityridae	Black-tailed Tityra *Tityra cayana*	P10	Outer primaries?	1.1	n/a	n/a	No	4
Tyrannidae	Vermillion Flycatcher *Pyrocephalis rubinoides*	P10	Outer primaries?	0.52	1	14.8	No	2?, 4
Tyrannidae	Scissor-tailed Flycatcher *Tyrannus forficatus*	P10	P10	1.8	1.9	11.6	Yes	
Tyrannidae	Western Kingbird *Tyrannus verticalis*	P10	Outer primaries	3	n/a	n/a	No	4
Eurylamidae	Comm.on Sunbird-Asity *Neodrepanis coruscans*	P10	P10	8.4	7	20.4	No	2, 3
Eurylamidae	African Broadbill *Smithornis capensis*	P5, P6, P7, P8, P9, P10	Outer primaries	0.8	1.4	19.6	Yes	
Eurylamidae	Rufous-sided Broadbill *Smithornis rufolateralis*	P5, P6, P7, P8, P9, P10	Outer primaries	1.1	1.8	18.0	Yes	
Fringilidae	‘Apapane *Himatone sanguinea*	P10	Outer primaries	0.4	3.1	15.6	No	1, 2, 4
Meliphagidae	Tui *Prosthamadera novaeseelandae*	P9	P9 (gap with neighbors)	0.6	3.9	15.4	No[4]	1, 2?, 4
Corvidae	Comm.on Raven *Corvus corax*	P7, P8, P9	Outer primaries?	0.5	n/a	n/a	No[4]	4

[1] If a feather produced multiple frequencies, e.g. as a function of airspeed, only the frequency closest to the flight sound is listed.

[2] When multiple feathers were tested, only one feather needed to match to be scored 'yes'

[3] Criteria:

1) Whether the flutter frequency matched (was within 25% of the 1st, 2nd or 3rd harmonic of flight sound (note: the 3rd harmonic matches are from snipe, which tend to produce harmonic stacks in which the dominant frequency was sometimes not the fundamental)

2) Whether the critical velocity (U*) was a realistic flight speed;

3) whether the feather region that fluttered was likely to flutter in the actual bird (for regions of flutter, see figure 3);

4) Whether the sound produced was loud, consistent, and easily repeated, and at a realistic feather orientation.

[4] Hypothesized false negatives; see results and discussion for further detail

Table S3. Sixty-nine hypothesized independent origins of mechanisms of sonations produced by feathers

Family	*Genus/Clade*	Hypothesized Mechanism[1]	Context
Anatidae	Ducks (*Anas spp.*)	AF	Aerial
Cracidae	Guans (*Pipile, Penelope, Penelopina, Aburria, Crax, Chamaepetes spp*)	S/C (?)	Aerial
Phasianidae	Ruffed Grouse (*Bonasa umbellus*)	Air pulses	Perched
Phasianidae	Greater Sage Grouse (*Centrocercus urophasianus*)	Rubbing	Perched
Phasianidae	Spruce Grouse (*Falcipennis canadensis franklinii)*	S/C	Perched
Phasianidae	Caucasian Black Grouse (*Tetrao mlokosiewiczi*)	AF	Aerial
Charadriidae	Double-banded Plover (*Charadrius bicinctus*)	S/C	Perched
Charadriidae	Northern Lapwing (*Vanellus vanellus*)	AF	Aerial
Scolopacidae	Snipe (*Gallinago* spp, *Coenocorypha* spp.)	AF (tail)	Aerial (dive)
Scolopacidae	Little Curlew *(Numenius minutus)*	AF	Aerial (dive)
Scolopacidae	Red Phalarope (*Phalaropus fulicarius)*	AF (females)	Perched?
Scolopacidae	American Woodcock (*Scolopax minor)*	AF	Aerial
Gruiformes	Lesser Florican (*Sypheotides indica)*	S/C (?)	Aerial (jump)
Gruiformes	Little Bustard (*Tetrax tetrax*)	AF	Aerial (jump)
Columbidae	Various doves (C*olumba palumbus*, *Stretopelia decaocto*)	S/C	Aerial
Columbidae	Crested Pigeon (*Ocyphaps lophotes*)	AF	Aerial
Strigidae	Owls (*Asio spp.* and relatives)	S/C	Aerial
Tytonidae	Barn Owl (*Tyto alba)*	S/C	Aerial
Caprimulgidae	White-winged Nightjar (*Eleothreptus candicans*)	Air pulses	Aerial
Caprimulgidae	Chuck-will's-widow and relatives (*Caprimulgus carolinensis*)	S/C	Aerial
Caprimulgidae	Nighthawks (*Chordeiles spp*.)	AF	Aerial (dive)
Caprimulgidae	Sickle-winged Nightjar (*Eleothreptus anomalus)*	WW	Aerial
Caprimulgidae	Ladder-tailed Nightjar *(Hydropsalis climacocerca*)	AF	Aerial
Trochilidae	Bee hummingbird clade (Mellisugini)	AF (tail)	Aerial (dive)
Trochilidae	Broad-tailed Hummingbird and relatives (*Selasphorus* spp.	AF (wings)	Aerial
Trochilidae	Ruby-throated Hummingbird and relatives (*Archilochus* spp.)	WW (wings)	Aerial

Trochilidae	Magenta-throated Woodstar and relatives (*Philodice sp.*)	S/C	Aerial
Trochilidae	Sabrewings (*Campylopterus spp.*)	S/C	Perched?
Trochilidae	Golden-bellied Starfrontlet (*Coeligena bonapartei*)	S/C	Aerial
Trochilidae	Trainbearers (*Lesbia spp.*)	S/C	Aerial (dive)
Trochilidae	Coquettes (*Lophornis, Popelairia spp.*)	AF	Aerial (dive)
Trochilidae	Jamaican Streamertails (*Trochilus spp.*)	AF	Aerial
Brachypteraciidae	Long-tailed Ground Roller *(Uratelornis chimaera)*	S/C	Perched
Todidae	Todies (*Todus spp.*)	WW	Aerial
Indicatoridae	Honeyguides (*Indicator spp.*)	WW	Aerial
Indicatoridae	Lyre-tailed Honeyguide *(Melechneutes robustus)*	AF (tail)	Aerial (dive)
Alaudidae	Flappet Larks, (*Mirafra spp.*)	S/C	Aerial
Cisticolidae	Cisticolas and Prinias (*Cisticola spp, Prinia spp.*)	S/C	Perched
Conopophagidae	Gnat-eaters (*Conopophaga spp*)	WW	Aerial
Cotingidae	Cotingas (*Cotinga spp, Ampelion rubrocristata*)	WW	Aerial
Cotingidae	Purple-breated Cotinga (*Cotinga cotinga*)	S/C	Aerial
Cotingidae	Cotingas (*Cotinga spp.)*	AF	Aerial
Cotingidae	Red Cotingas (*Phoenicercus spp.*)	AF	Aerial
Drepaniidae	Honeycreepers. (*Himatione sanguinea, Vestiaria coccineai*)	WW	Aerial
Eurylaimidae	Broadbills (*Smithornis spp.*)	AF	Aerial
Eurylaimidae	Sunbird-asities (*Neodrepanis spp.*)	AF	Aerial
Furnarinidae	Buff-winged Cinclodes (*Cinclodes fuscus*)	AF	Perched?
Icteridae	Oropendolas (*Psarocolius spp.*)	S/C	Aerial
Meliphagidae	*Anthornis melanura, Prosthemadera novaseelandiae*	AF	Aerial
Paradisaeidae	Birds of Paradise (various genera)	Rustling	Perched
Paradisaeidae	Superb Bird-of-Paradise (*Lophorina superba*)	S/C	Perched
Phyloscopidae	Arctic Warbler (*Phylloscopus borealis*)	S/C	Perched?
Pipridae	Various manakins (*Corapipo, Ilicura, Pipra, Manacus, Chiroxiphia caudata*)	S/C	Perched or Aerial

Pipridae	Lance-tailed Manakin (*Chiroxiphia lanceolata*)	Whoosh	Aerial
Pipridae	Club-winged Manakin (*Machaeropterus deliciosus*)	Stridulation	Perched
Pipridae	Various manakins	WW	Aerial
Pipridae	*Manacus* manakins	Rustling	Aerial
Pipridae	*Heterocercus* manakins	AF (tail)	Aerial (dive)
Pittidae	Pittas (*Pitta spp.*)	AF	Perched?
Promeropidae	Sugarbirds (*Promerops spp.*)	S/C	Aerial
Thraupidae	Blue-black Grassquit (*Volatinia jacarina*)	S/C	Aerial (jump)
Tityridae	Becards (*Pachyramphus spp*.)	S/C	Aerial?
Tityridae	Tityras (*Tityra spp.*)	WW	Aerial
Tyrannidae	Various flycatchers, including *Alectrurus*, *Arundinicola, Lessonia*, and *Mionectes*	WW	Aerial
Tyrannidae	*Atalotriccus*, *Knipolegus*,and *Musciasaxicola* spp.	S/C	Aerial?
Tyrannidae	Twistwings (*Cnipodectes spp.*)	AF	Aerial
Tyrannidae	Pihas, (*Lipaugus spp*)	AF	Aerial
Tyrannidae	Scissor-tailed Flycatcher (*Tyrannus forficatus*)	AF	Aerial
Tyrannidae	Kingbirds (*Tyrannus spp.*)	WW	Aerial

[1] See Table S1 for references.

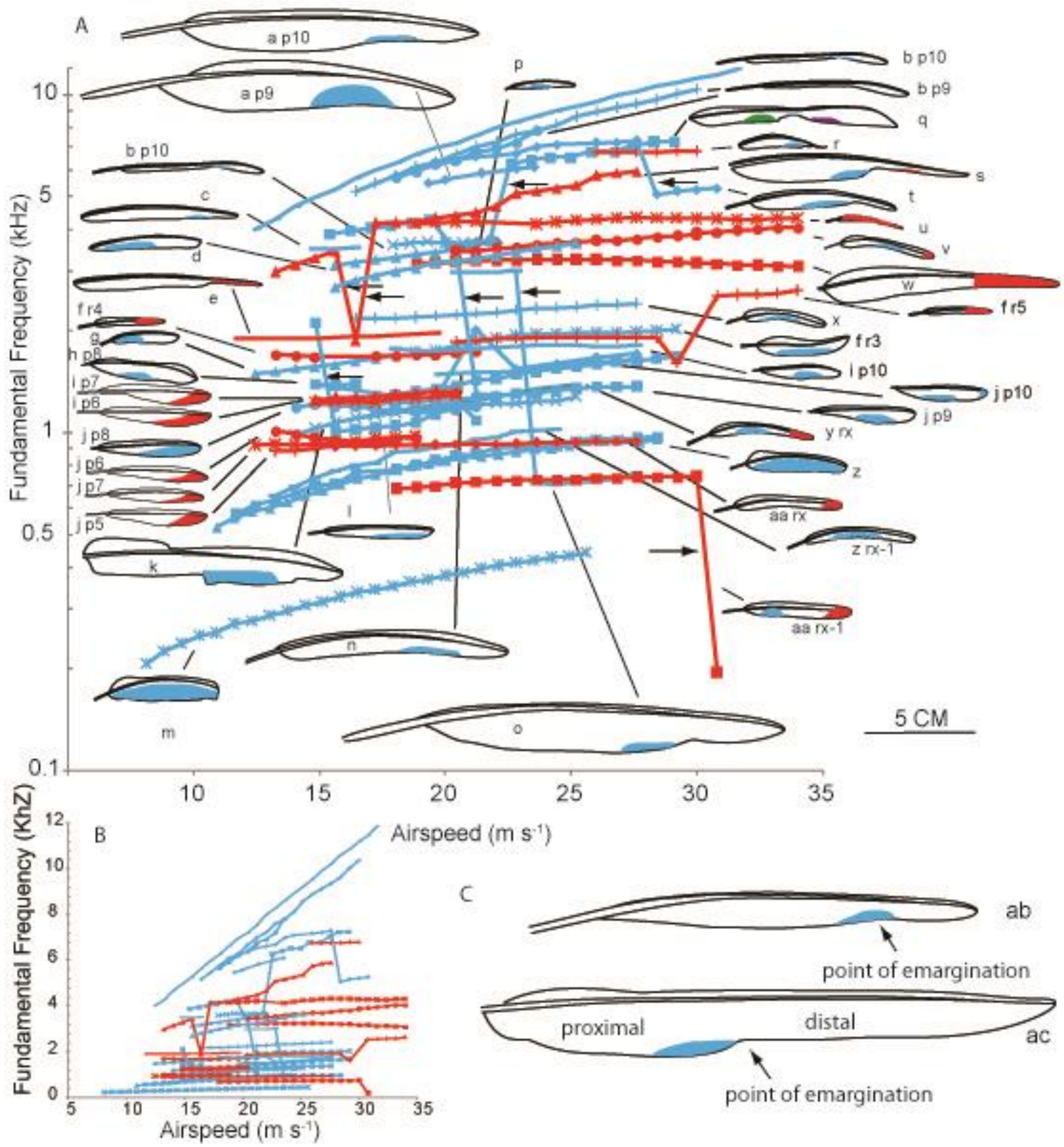
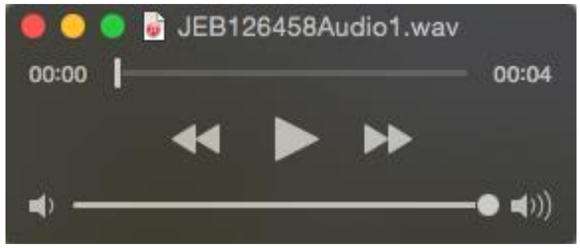


Fig. S1, an expanded version of Fig. 1: Flutter fundamental frequency against airspeed for 43 feathers (**A, B**). In **A**, note log Y-axis; **B** shows same data on linear Y axis. (**C**) two examples of the point of emargination. All line drawings of individual feathers are to 5cm scale bar. Color patches show approximate regions and mode of flutter: red = tip, blue = trailing vane, green and purple indicate feathers that exhibited simultaneous modes at alternate frequencies, which were ignored. Arrows in **A** indicate abrupt changes in frequency caused by mode jumps (some mode jumps not indicated due to figure clutter). First letters indicates species, second letter indicates feather if multiple feathers were measured; primaries, P5 - P10 and rectrices, R2 - R6, except in

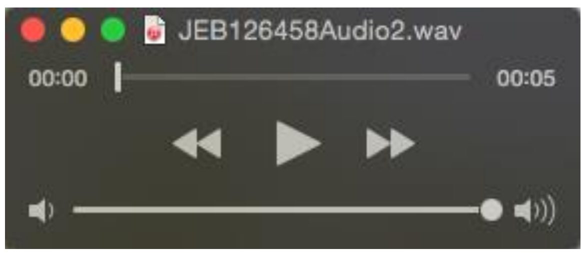
Journal of Experimental Biology • Supplementary information

snipe (*Gallinago* spp.) where rx = outermost rectrix, rx-1 = second to outermost rectrix, because snipe have variable numbers of tail-feathers (Tuck, 1972).

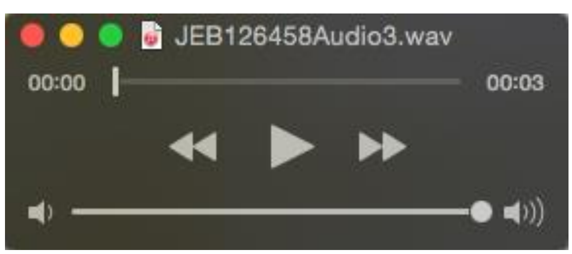
a: *Beucephala islandica*, b: *Scolopax minor*, c: *Cotinga cotinga* P10; d *Himatione sanguinea* P10; e: *Tyrannus forficatus* P10; f: *Melechneutes robustus*; g: *Todus mexicanus* outer primary (ID uncertain); h: *Conopophaga lineata* P8; i: *Smithornis rufolateralis*; j: *S. capensis*; k: *Tetrax tetrax* P7; l: *Pyrocephalus rubinus* p10; m: *Gallinago gallinago* rx; n: *Zenaida macruoura* P10; o: *Anas americana* P10; p: *Neodrepanis coruscans* P10; q: *Prosthamadera novaseelandae* P7; r: *Phoenicercus carnifex* P7; s: *Sypheotides indicus* P10; t: *Leptoptila verreauxi* P10; U: *G. stenura* rx-1; v: *G. nemoricola* rx; w: *Ocyphaps lophotes* p8; x: *G. paraguiae* rx; y: *G. megala*; z: *G. delicata* rx; aa: *G.jamesoni*; ab: *Anas strepera* P10; ac: *Corvus corax* P8. No data shown for aP10, ab or ac, as these tended to exhibit chaotic flutter without a discrete fundamental frequency.



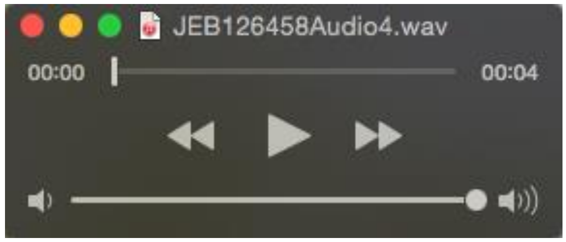
Audio 1. Sound of a falcon (*Falco peregrinus* or *F. mexicanus*) in pursuit of a large dove in Jeff Davis County, Texas, USA, May 2010, recorded by CJC.



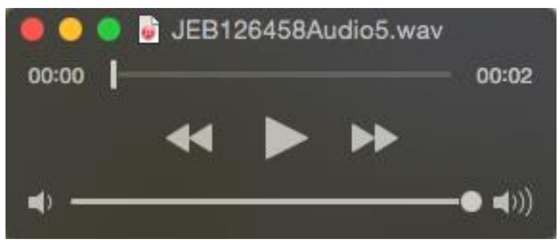
Audio 2. Flock of roughly 50 band-tailed pigeons (*Patagioenas fasciata*) flying overhead in Sololá Department, Guatemala, October 2010, recorded by CJC.



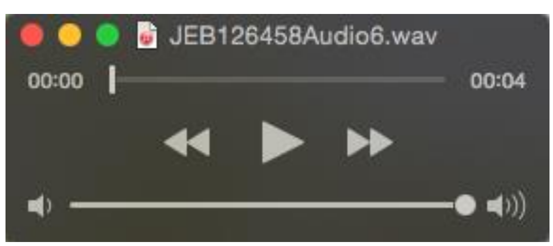
Audio 3. Male black-tailed trainbearer (*Lesbia victoriae*) performing a flight display in Cundinamarca Department, Colombia, January 2010, recorded by CJC.



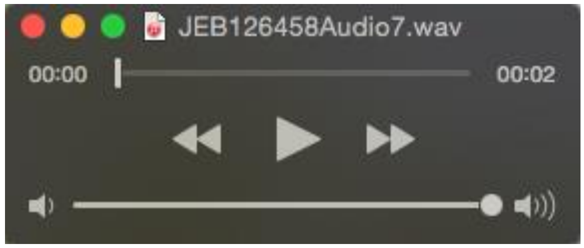
Audio 4. Male booted racket-tail (*Ocreatus underwoodii*) performing a flight display to a female in Pinchincha province, Ecuador, April 2011, recorded by CJC.



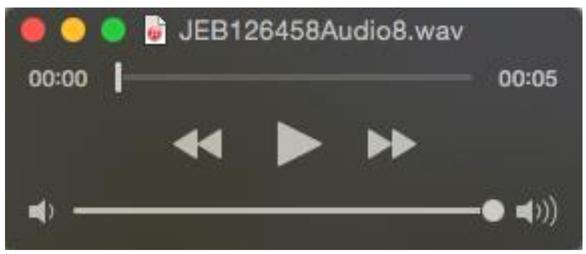
Audio 5. Male wire-crested thorntail (*Discosura popelairii*) performing a flight display to a female in Napo province, Ecuador, September 2011, recorded by CJC.



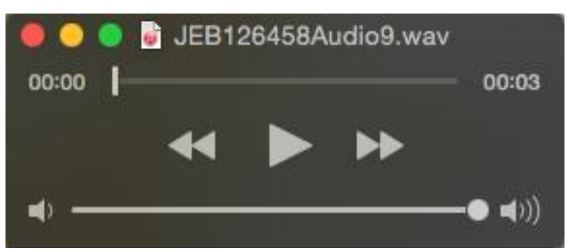
Audio 6. Black-and-white-casqued hornbill (*Bycanistes subcylindricus*) of unknown sex flying overhead in Bundibugyo District, Uganda, July 2011, recorded by CJC.



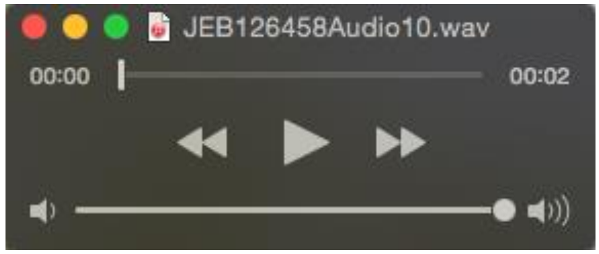
Audio 7. Black vulture (*Coragyps atratus*) of unknown sex flying overhead in Sacatapéquez Department, Guatemala, October 2010, recorded by CJC.



Audio 8. Eared dove (*Zenaida auriculata*) of unknown sex taking flight in response to the approach of a human, in Cundinamarca Department, Colombia, January 2010, recorded by CJC.



Audio 9. Male Cuban tody (*Todus multicolor*) performing an apparently agonistic flight display, in response to conspecific playback in Matanzas Province, Cuba, April 2012, recorded by CJC.



Audio 10. Male vermillion flycatcher (*Pyrocephalus rubinus*) performing a flight display during dawn song in Valle del Cauca Department, Colombia, January 2010, recorded by CJC.

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