

High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves)

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Summary

Basic kinematic and detailed physical mechanisms of avian, non-vocal sound production are both unknown. Here, for the first time, field-generated high-speed video recordings and acoustic analyses are used to test numerous competing hypotheses of the kinematics underlying *sonations*, or non-vocal communicative sounds, produced by two genera of Pipridae, *Manacus* and *Pipra* (Aves). Eleven behaviorally and acoustically distinct sonations are characterized, five of which fall into a specific acoustic class of relatively loud, brief, broad-frequency sound pulses, or *snaps*. The hypothesis that one kinematic mechanism of *snap* production is used within and between birds in general, and manakins specifically, is rejected. Instead, it is verified that three of four competing hypotheses of the kinematic mechanisms used for producing *snaps*, namely: (1) above-the-back wing-against-wing claps, (2) wing-against-body claps and (3) wing-into-air flicks, are employed between these two clades, and a fourth mechanism, (4) wing-against-tail feather interactions, is discovered. The kinematic mechanisms used to produce *snaps* are invariable within

each identified sonation, despite the fact that a diversity of kinematic mechanisms are used among sonations. The other six sonations described are produced by kinematic mechanisms distinct from those used to create *snaps*, but are difficult to distinguish from each other and from the kinematics of flight. These results provide the first detailed kinematic information on mechanisms of sonation in birds in general, and the Pipridae specifically. Further, these results provide the first evidence that acoustically similar avian sonations, such as brief, broad frequency *snaps*, can be produced by diverse kinematic means, both among and within species. The use of high-speed video recordings in the field in a comparative manner documents the diversity of kinematic mechanisms used to sonate, and uncovers a hidden, sexually selected radiation of behavioral and communicative diversity in the Pipridae.

Movies available on-line

Key words: *Manacus*, *Pipra*, sonation, kinematics, acoustic communication, courtship display.

Introduction

Although studies of the mechanisms of sound production in arthropods have a rich history (Dumortier, 1963; Haskell, 1974; Bennet-Clark, 1975), and have increased in recent years (Bennett-Clark and Young, 1992; Desuttergrandcolas, 1995; Conner, 1999; Versluis et al., 2000; Yack, 2000; Burrows, 2001; Patek, 2001), similar studies of non-vocal sound production among some of the most acoustically oriented organisms, birds, are almost non-existent. While birds are renowned for vocalizations, many also communicate acoustically by non-vocal means. Darwin (1871) dedicated eight pages of discussion to the significance of these sounds in birds, which he called ‘instrumental music’, but more recently are referred to as ‘mechanical sounds’ (Manson-Barr and Pye, 1985; Prum, 1998). We here propose and apply the term *sonation*, to emphasize the distinction between these sounds

and vocalizations, and to create a companion verb, to *sonate*, that refers to the act of producing non-vocal acoustic signals. Thus, avian sonations are intentionally modulated, communicative acoustic signals, produced using non-syringeal structures such as the bill, wings, tail, feet and/or body feathers.

Several characteristics of avian sonations have prevented research on sound production mechanisms. Sounds are usually produced in behavioral contexts that are difficult to induce in captivity, often during flight, using motions too rapid to be seen by the unaided eye or conventional-speed video recording, and by species in remote and/or restricted localities around the world. These factors, combined with the fact that many birds are prohibitively difficult to obtain, maintain and manipulate in laboratory settings, have prevented mechanism-oriented studies of this class of communicative signals in birds.

Nonetheless, sonations play important roles in many species' behavioral repertoires: they are frequently used in concert with vocalizations for territorial maintenance (Aubin, 1972; Winkler and Short, 1978; Miller and Inouye, 1983; Craig, 1984; McBurney, 1989), or in polygynous or lek-breeding species as elements of complex courtship displays (Prum, 1998). Morphologically, birds use diverse structures for sound production, and feather modifications have been described for many species known to sonate (overviews by Darwin, 1871; Manson-Barr and Pye, 1985; Prum, 1998; Bostwick, in press).

The most extreme development of the use of sonation is found in the Neotropical manakins, the Pipridae (Prum, 1998). The Pipridae include approximately 40 species of polygynous, lek-breeding, sexually dimorphic birds found in the tropical forests of Central and South America. Male manakins perform elaborate courtship displays, and over half of the species sonate during these displays (Prum, 1998). Phylogenetic analyses of the Pipridae indicate numerous independent evolutionary origins of sonation within the family, and extensive evolution within piprid genera and species (Prum, 1998; Bostwick, 2000). Included among the diversity of piprid sonations are several acoustic classes of sounds, the most common of which are brief, broad-frequency pulses (Prum, 1998).

Because many bird species sonate using their wings (Manson-Barr and Pye, 1985; Prum, 1998), hypotheses of sound-producing mechanisms have been proposed previously, and an examination of the literature yields two basic acoustic classes with accompanying mechanistic hypotheses. The first class includes relatively loud, brief, broad-frequency (or toneless) sounds, variously referred to as *snaps*, *clicks*, *claps* or *cracks*. Many species are known to *snap* with their wings (Chapman, 1935; Skutch, 1949, 1969; Sick, 1959; Snow, 1962, 1963, 1977; Payne, 1973; Bertram, 1977; Schwartz and Snow, 1978; Robbins, 1983; Bomford, 1986; Sankaran, 1996; Prum, 1998; Tello, 2001), and competing, speculative hypotheses of the kinematic mechanisms behind wing *snaps* include: (1) wing-to-wing claps above the body, (2) wing-to-wing claps below the body, (3) wing-to-body claps, (4) striking together of adjacent secondary feathers or (5) sudden interruption of air-flow between wing-flaps (for a review, see Bostwick, in press). None of these hypotheses have been critically examined or tested. The second class of wing-generated sonations includes a variety of airy, pulsed and tonal sounds produced in flight, variously referred to as *whistles*, *humms* or *whirrs*. These are universally attributed to vibrations induced in flight feathers when air is forced through them at relatively rapid speeds (Miller, 1925; Pettingill, 1936; Carr-Lewty, 1943; Tuck, 1972; Craig, 1984; Miskelly, 1990). This hypothesis, while reasonable, is supported by little experimental data, and an alternative hypothesis proposed here, of friction among feathers, has not been considered (for a review, see Bostwick, in press).

Extreme modifications of wing morphology (Lowe, 1942; Schultz et al., 2001; Bostwick, 2002) and physiology (Schultz and Schlinger, 1999; Saldanha et al., 2000) have been

documented in several sonating piprids, especially the genus *Manacus*, but the function of the morphological modifications has remained unexplained due to lack of information on the mechanisms of sound production. The goal of the research presented here was to test the mechanistic hypotheses delineated above in order to understand the functional role of the modified piprid wing morphology. To this end, we distinguish between two levels of mechanistic description: (1) kinematic mechanisms, or the gross-level motions of the body and limbs used to sonate, vs. (2) physical mechanisms, or the finer-level interactions of structures with air that create sound. We here test several sonations for congruence with one of four kinematic hypotheses (modified from above): (1) wing-to-wing claps above the body, (2) wing-to-wing claps below the body, (3) wing-to-body claps and (4) wing flicks into air. These hypotheses make obvious, non-overlapping predictions about observed motions of the wings relative to each other and the body. Identifying the fundamental kinematic mechanisms underlying sound production will better enable functional interpretation of morphological modifications found in piprids. Three competing hypotheses of the physical mechanisms of sound production are suggested for wing *snap* sonations, and are examined here preliminarily: (1) percussion (created by forceful contact between solid objects), (2) whip-like sonic booms (created when an object moves faster than the speed of sound), and (3) vacuum-created pressure claps (created when a low pressure center is suddenly collapsed). Contact between two solid structures is a minimum critical prediction for a percussive mechanism. Extremely rapid motion of a structure through air is necessary for either the whip or vacuum mechanisms, with the whip mechanism requiring motions faster than the speed of sound. The absence of these respective actions during sound production amounts to rejection of these respective hypotheses.

Representatives from two lineages of piprid hypothesized to have evolved sonation independently, *Manacus* and *Pipra* (Prum, 1998; Bostwick, 2000), are examined in detail. Many behaviorally and acoustically distinct sonations have been recognized in, and are shared by, the four species in the genus *Manacus* (Chapman, 1935; Snow, 1962; Skutch, 1969). The sonations of *Manacus* will be referred to as follows: (1) *snaps*, (2) *rolls* or *roll-snaps*, (3) *snorts*, (4) *whirrs*, (5) *rattles* and (6) *fanning* (terms used previously in the literature; see Chapman, 1935; Snow, 1962; Skutch, 1969). The mechanical sounds of *Pipra mentalis* have been described in less detail; however, both of the two classes of sounds described above have been recognized: a low-frequency *hum*, and brief, broad frequency *snaps* used in multiple behavioral contexts (*poops* and *kloks*, respectively; Skutch, 1949, 1969).

Recent advances in high-speed video technology make it possible to record sonation kinematics in field conditions (Dalton, 2002). Here we report the results of the analysis of high-speed video-recordings of *Manacus* and *Pipra* wing-sound production in wild and captive conditions. We verify the non-vocal nature of the sounds, analyze the acoustic characteristics of each sonation observed, distinguish the

behavioral contexts in which different sounds are produced, and delineate the gross-level kinematics behind sound production where possible. We test each of four kinematic hypotheses of sound production, and make preliminary examinations for each of three physical hypotheses, for each of several *snap* sonations. In doing so, we uncover a previously unknown radiation of mechanistic diversity for sound-production in birds.

Materials and methods

Video and audio recording

Four species were recorded from two independent sound-producing clades (Prum, 1998): *Manacus manacus* Linnaeus 1766, *M. aurantiacus* Salvin 1870 and *M. candei* Parzudake 1841 representing the *Manacus* clade, and *Pipra mentalis* Sclater 1857 representing the *Pipra* clade.

Two video cameras recorded simultaneously: a digital camcorder (with both NTSC standard and progressive scan recording modes) to record sound and behavior simultaneously, and a high-speed digital video camera to capture the details of sound-producing motions. The conventional Sony DCR VX2000 miniDV camcorder (Tokyo, Japan) was used with a 1.7 \times teleconverter lens, and shutter speeds of 1/60–1/2500 s (as permitted by light conditions). Recordings were made using Sony's progressive scan recording mode, which captures 15 full (all pixels) images per second. A high-speed Redlake MotionMeter digital video camera (San Diego, CA, USA) was used with a 28–70 mm 1–2.8f zoom lens, recording speeds of 60, 125, 250, 500 and 1000 frames per second, and shutter speeds of 1/60–1/4000 s. Individual video frames, taken from simultaneous recordings with the Sony and high-speed video cameras, were visually aligned to provide maximum synchronization with the Sony audio recordings to within 1, 2 or 4 ms (for high-speed recordings at 1000, 500 and 250 frames per second, respectively). This resolution was sufficient for description of the overall kinematics of sound production and distinguishing between alternative kinematic hypotheses, but it was not sufficient for determining the exact moment of sound production, and thus distinguishing between competing hypotheses of physical mechanisms of sound production. Acoustic samples were augmented with additional tape recordings made with a Sony TCM5000 cassette recorder and a Sennheiser ME80 (Wedemark, Germany) microphone.

Two captive individual males of *M. manacus* were recorded at the San Diego Zoo (1 March, 2001) and San Diego Wild Animal Park (28 February – 5 March, 2001). Two wild individuals of *M. candei* were recorded in La Selva Biological Reserve, Prov. Heredia, Costa Rica, on 13–15 March, 2001. Wild *M. aurantiacus* were recorded in Carara National Park, Prov. Puntarenas, Costa Rica on 23 March, 2001. Displays and sonations in *M. aurantiacus* appeared identical to those of other *Manacus* species and therefore were only recorded by conventional video. Recordings of at least four individual male

P. mentalis were made in La Selva Biological Reserve, Prov. Heredia, Costa Rica, at 800–850 m on 9–15 March, 2001.

Video and audio analysis

Male manakins display and sonate incessantly during the breeding season (Snow, 1962; Skutch, 1969; Robbins, 1983; Bostwick, 2000). Accordingly, the observed individuals sonated dozens of times an hour, from 07:00 h–13:00 h, daily, during the 14 days of video-recording. As is common with vocalizations in birds, each sonation type was audibly distinct and easily identifiable, and the behavioral contexts in which individual sonation types were employed were non-overlapping. Attempts were made to record each sonation from numerous perspectives to best characterize the motions involved in sound production. Video footage was edited in iMovie 2 (Apple Computer, Inc., Cupertino, CA, USA), and organized by species and sonation type. Acoustic and kinematic analysis (below) showed that the acoustic properties and kinematics for each sonation are distinct from each other, congruent with the field-based distinctions. Sample sizes of the high-speed video recordings examined to characterize the kinematics of each sonation type vary and are given with each sonation description (below). Durations of sound-producing behaviors were calculated from the frame numbers and recording speeds.

Acoustic samples of each distinct sonation were taken from video and audio recordings and analyzed in Canary 1.2.1 (Charif et al., 1995). Sample sizes varied with the frequency at which the sounds were produced and recorded. Variables such as number of sound pulses or notes, intervals between pulses, and peak (or most powerful) frequency were measured for each sound as appropriate. The majority of the sonations described are characterized by being very brief, broad-frequency pulses. Pulse duration and frequency range are inherently difficult to characterize in such sounds (Bradbury and Vehrencamp, 1998), a problem exacerbated by the variety of recording conditions experienced in the field. Therefore, we only report measurements of pulse duration, or peak frequency, of these brief, broad-frequency pulses, for sounds in which these measures are reproducible. Measurements of homologous sounds from each of the three species of *Manacus* were initially analyzed separately. Analyses of variance (ANOVAs) were run on species means of pulse number and inter-pulse interval for the four potentially variable sonations produced by *Manacus*, only one of which varied significantly. Therefore, with the exception of this one variable (*rattle* interpulse interval), *Manacus* sound measurements are pooled among the three species. Values are given as means \pm s.d. and range.

Results

All three *Manacus* species produce five acoustically and behaviorally distinct sonations: the *snap*, *roll-snap*, *snort*, *rattle* and *whirr*. *Manacus manacus* makes a sixth sound called *fanning*. Each male sonates from within his territory among a lek of males (Chapman, 1935; Snow, 1962; Skutch, 1969).

Two sounds, the *snap* and the *snort*, are produced on the male's display court, whose structure, a cleared area of forest floor (~1 m²) that is bordered by 2–5 small (1–2 cm diameter) upright saplings spaced 0.5–1.5 m apart (Chapman, 1935), is intimately related to the behavioral production of the sounds. The other sounds, the *roll-snap*, *rattle*, *whirr* and *fanning*, are generally produced within the territory but not directly on the court itself. The acoustic and kinematic descriptions below are representative of all three species unless indicated otherwise.

Pipra mentalis also produces five distinct sonations, here named the *click*, *rub-snap*, *clap*, *hum* and *swoop*. Male *P. mentalis* also display within lek territories, typically on one or two main display perches in the sub-canopy 7–20 m from the ground (Skutch, 1969; Prum, 1990). Three sounds, the *click*, *rub-snap* and *clap*, are performed while perched. The other two sounds, the *swoop* and *hum*, are performed in flight. Three of the sonations, *clicks*, *humms* and *rub-snaps*, are produced together in stereotyped sequence in to-and-fro display flights (*sensu* Prum, 1990). The to-and-fro display entails two short (1–2 m) flights away from and then back to the main display perch of the male. Each of the two flights is preceded by a *click*, accompanied by a *hum*, and the display ends with one *rub-snap* after the return flight ($N>50$). The timing of these elements are: *click-to-humms* 25.35 ± 0.77 ms (range 23.90–26.30 ms; $N=20$); 1st *click* to 2nd *click* 1095.2 ± 152.0 ms (854.0–1328.0 ms; $N=17$); 2nd *click* to *rub-snap* 711.2 ± 87.8 ms (564.0–854.0 ms; $N=19$).

Each sonation is described separately, with the acoustic characteristics described first, followed by kinematic descriptions, and finally the proposed kinematic and physical mechanisms where possible. Five sonations, the *snap*, *roll-snap*, *click*, *rub-snap* and *clap*, are acoustically similar in being loud, brief, broad frequency *snaps*, and these are described first. The kinematics involved in the production of the six non-*snap* sonations, the *snort*, *rattle*, *whirr*, *fanning*, *hum* and *swoop*, are, in general, more difficult to characterize and therefore are only discussed briefly.

Snap sonations

Snap: Manacus

The sound is a sharp, powerful *snap* or whip-like *crack*. Acoustically, it is a single powerful, brief, broad-frequency pulse of sound (Fig. 1). The peak, or most powerful, frequency of a pulse is 4.61 ± 0.90 kHz (2.80–6.12 kHz; $N=57$).

The *snap* is produced while the male is airborne by clapping

the dorsal surfaces of the wings together above the back of the bird ($N=28$ high-speed recordings). The male perches horizontally near the base of a vertical sapling bordering his display court in preparation for a spring/*snap* across the court to another vertical sapling. First he crouches against the sapling-perch, his back facing the direction in which he is

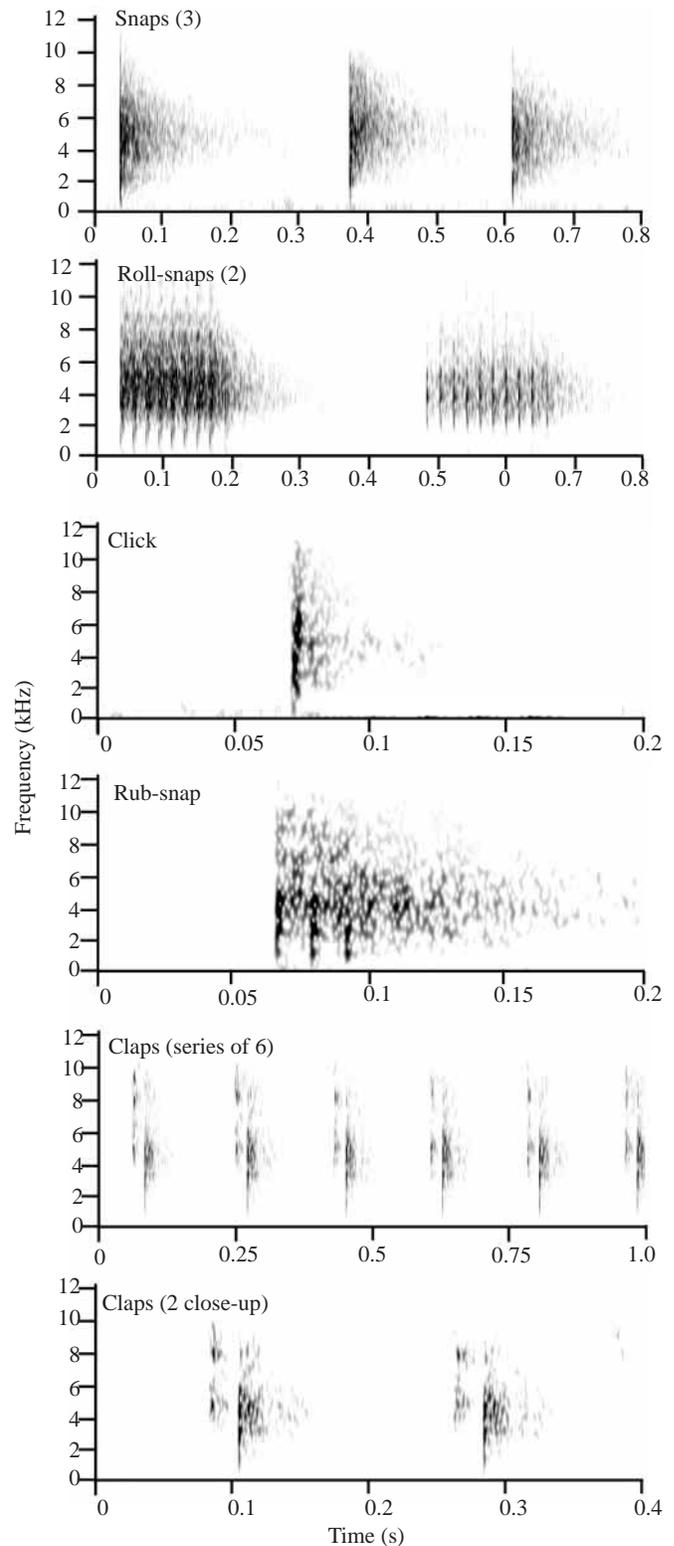


Fig. 1. Spectrograms of five *snap* sonations*. From top to bottom as labeled: three *snaps* (*M. candei*); two *roll-snaps* (nine and ten pulses respectively, from birds at different distances from recorder, *M. candei*); a *click* (*P. mentalis*); a *rub-snap*, showing the characteristic three sound pulses (*P. mentalis*); a full series of six *claps*, demonstrating the overall timing and pattern of *claps* (*P. mentalis*); two *claps* on an expanded time axis to show the relationship of the first and second pulses of sounds within each *clap*. Detailed descriptions of motions are given in the text. *Note variation in time-axis scale among spectrograms.

about to spring (Fig. 2.1). While crouching, he first supinates his humerus, rotating it outward along its long axis; this action has the effect of elevating the wrists slightly above his back (Fig. 2.2). Next he extends his legs to launch himself forcefully from the perch (Fig. 2.3). As he springs, back first, he extends his wrist and elbow joints so that his wings form a flat plane across his back (as if in a 'soaring' position, Fig. 2.3,4). After leaving the perch, he rapidly adducts his open wings over his back by rapidly retracting and further supinating the humerus. This action forcefully claps together the dorsal surfaces of the wrist joints, approximately where the bases of the remiges insert (Fig. 2.5,6). The male then rotates the leading edge of the wing outward in a pronating motion (Fig. 2.7–2.8). Finally, the wings are either closed to a resting position at the sides, or begin a downstroke that determines the subsequent maneuvering of the male's body (Fig. 2.9,10), before he alights on a neighboring vertical perch. All wing-to-wing contact occurs as the male sails through the air from the momentum of his jump between perches.

Kinematically, the *snap* is produced using a wing-against-wing clap of the dorsal surfaces of the wings above the male's body, consistent with hypothesis 1 (see Introduction). The kinematics observed eliminate the alternative hypotheses of (2) wing-to-wing percussion below the body, (3) wing-to-body claps and (4) wing flicks into air, as none of the motions predicted for these alternative hypotheses are observed. None of the three hypotheses of the physical mechanism of sound production can be eliminated: the sound may be produced either by percussion (of the wrists, flight feather bases, or more distal parts of the secondary feathers), or by a whip-like or collapsing vacuum mechanism possibly produced when the tips of the flight feathers whip through the air as a result of wing collision. The wrist contact is distinctly observable on the video, and is powerful, as indicated by the way with which the wing reverberates from this contact. Contact appears to occur near the swollen bases of modified secondary feathers, thus supporting a percussive mechanism of sound production. The nature of wing contact and feather motions subsequent to the collision of the wrists and swollen feather bases is difficult to discern, and may be a by-product of the pronating motion involved in wing recovery.

Roll-snap: *Manacus*

The *roll-snap* sounds like a loud, drawn-out, explosive, *crackkkkk!* Acoustically, it is a rapidly delivered series of pulses of sound each of which is similar in structure to the *snap* (Fig. 1). *Roll-snaps* include 7.10 ± 3.0 pulses (3–14 pulses; $N=31$). Intervals between the *snap* pulses in a *roll-snap* are 19.91 ± 1.1 ms (17.85–22.48 ms; $N=29$). Peak pulse frequency is 3.95 ± 0.67 kHz (2.24–5.24 kHz; $N=29$).

The fundamental motion used to produce *roll-snaps* is the same one used to produce *snaps*; the dorsal surfaces of the wings are struck together above the back. However, the male remains perched on a horizontal branch for the duration of the sonation, and since sound production involves a rapidly repeated train of pulses, the set-up and recovery of the wing form a repeatable cycle ($N=11$ high-speed recordings).

A perched male leans forward and elevates his wrists through humeral supination (Fig. 3.2). He momentarily opens his wings laterally into a 'soaring' position by extending the elbow and wrist joints (Fig. 3.3–5), before he then raises and retracts his open wings rapidly above his back, leading with the wrist, adducting them until the wrists forcefully collide (Fig. 3.6–9), as in *snap* production. The wing is then pronated, pulling the leading edges of the wings apart, while the tips of the flight feathers continue to move medially towards each other. As the distal tips of the flight feathers nearly meet, the wrists have reached their full lateral extent (Fig. 3.9–16). The wing is then supinated and retracted, bringing the wrists together again to collide, making the second pulse of sound, and swinging the tips of the flight feathers outwards (Fig. 3.16–19). This motion is repeated once for each *snap* pulse in the *roll-snap*. During this activity, the head, body and tail remain motionless, and the extension of the elbow and wrist joints remains constant. All motion is limited to the orientation of the wings, which swivel inward and outward around the shoulder joint, above the body, in a graceful, cyclic motion.

Kinematically, the sound pulses in a *roll-snap* are produced by a series of the same, above-the-body, percussive, wing-against-wing movements that *Manacus* uses to produce single *snaps*. As with single *snaps*, sound-generation appears to occur physically by the percussive wing contact, but the alternative hypotheses cannot be eliminated.

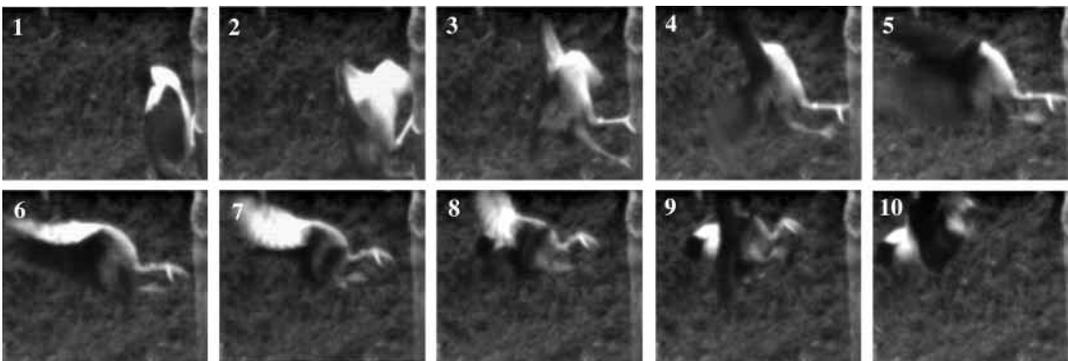


Fig. 2. Posterior view of *M. manacus* producing a *snap*. The perch is on the extreme right of the images; the background of each image is the floor of the males' court. Intervals between frames are 4 ms. Sound production occurs while airborne between frames 5 and 6.

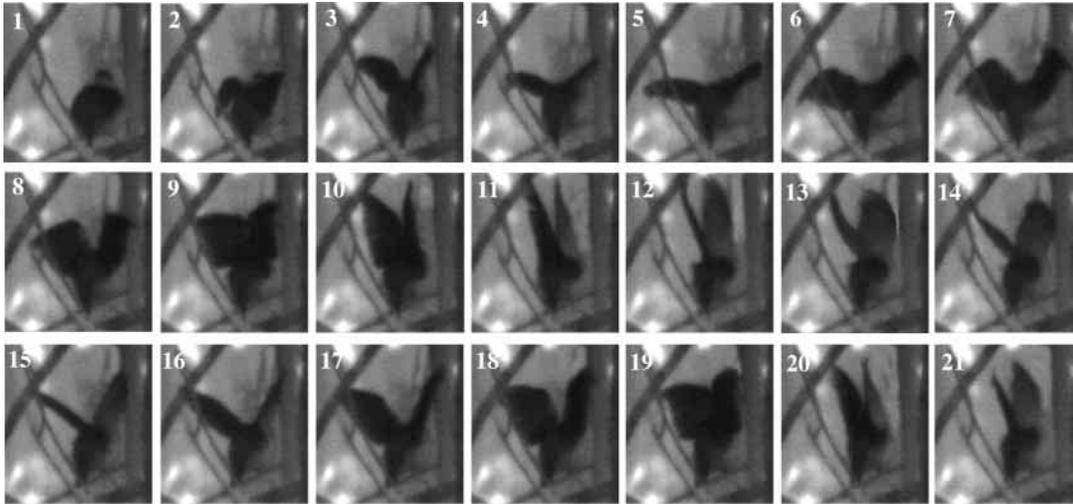


Fig. 3. Posterior view of *M. candei* producing two sound pulses of a *roll-snap*. Intervals between preliminary motions depicted in frames 1–5 are 4 ms; between frames 6 and 21 are 2 ms. Sound production occurs at frames 9 and 19.

Click: Pipra mentalis

This sound is a simple woody *click*, somewhat like two chopsticks being hit together. Acoustically, the *click* is lower in amplitude than the *snap* of *Manacus*, but is a similarly brief, broad frequency pulse (Fig. 1). Unlike the *snaps* of *Manacus*, these pulses exhibit variation in the amplitude of different frequencies, although variation in quality of recordings made it difficult to characterize these patterns. Peak pulse frequency is 4.81 ± 1.26 kHz (2.33–7.45 kHz; $N=26$), and the duration of the *click* pulse was 3.57 ± 0.50 ms (2.18–4.50 ms; $N=26$).

Clicks are produced during a lateral wing flick and recovery prior to the male's departure from a perch ($N=22$ high-speed recordings). Preliminary wing movement for the *click* involves an extended set of motions (Fig. 4). The bird first rotates the humerus, abducting and raising the wrist joints, and then extends the wrist and elbow joints to open the wings above the back (Fig. 4.1–7). The raised wings are then protracted and depressed as if beginning a downstroke for flight (Fig. 4.7–10). However, unlike a downstroke for propulsive flight, this downward motion continues only until the wing tips are fully stretched laterally to the side of the body in a flat plane (Fig. 4.11) before the wings are drawn in (the wing tips are never depressed below the level of the bird's body, Fig. 4.12–16). Next, the wings are drawn in while the bird

begins leaning forward and starts to extend his legs in preparation for flight (Fig. 4.17). Once the wings are fully retracted, the bird then elevates them again to begin the first propulsive downstroke, at which point the male finally leaves the perch (Fig. 4.17–24).

Since there is no wing-to-wing percussion, nor any wing-to-body percussion, these data support only one of the four competing kinematic hypotheses, the lateral wing-flick into the air. None of the three physical hypotheses can be eliminated; the sound may be made by collisions between adjacent feather rachii as the laterally extended wing is suddenly adducted toward the body, or alternatively, as the wing feather tips move rapidly through the air, an air compression/expansion mechanism may generate the sound, or a sonic whip-like mechanism.

Rub-snap: Pipra mentalis

The *rub-snap* sounds like a harsh, static-electric *churt*. Acoustically the *rub-snap* is composed of three brief, powerful, broad-frequency pulses produced in very rapid series (Fig. 1). No variation in the number of pulses was observed ($N=64$). Intervals between the pulses are approximately 13.40 ± 1.02 ms (12.40–17.51 ms; $N=32$). Peak pulse frequencies were 4.45 ± 1.22 kHz (2.84–7.60 kHz; $N=20$).

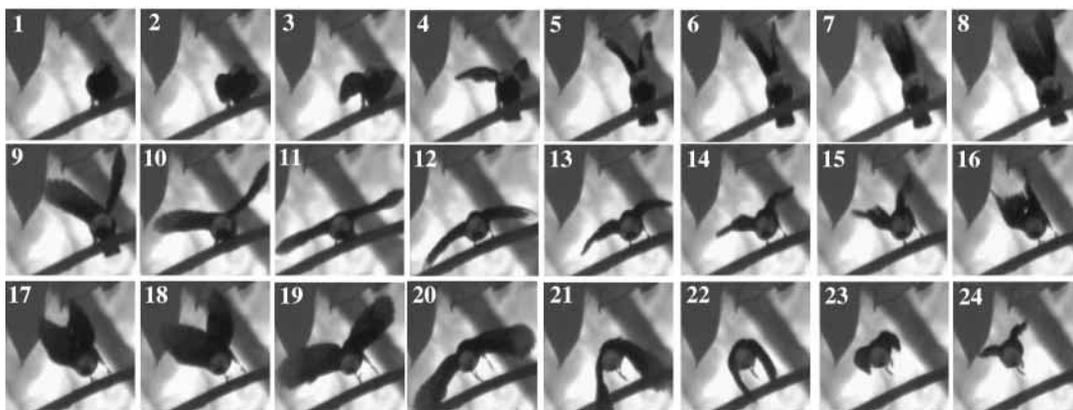


Fig. 4. Anterior view of *Pipra mentalis* producing a *click*. Intervals between frames are 4 ms. Sound production occurs at the frame 11; a propulsive wing beat spans frames 16–24.

This sound is produced while the bird is perched when the wing feather tips are rubbed down the sides of the tail in three rapidly repeated cycles ($N=19$ high-speed recordings). The wrist and primaries of each wing are first depressed along the sides of the body (Fig. 5A,B,2,3), which causes the tips of the primaries to slide across the base of the fanned tail (Fig. 5A,B,3–5), and then the still-flexed wing is abducted slightly outward and elevated in a recovery stroke (Fig. 5A,B,5–7). This motion is repeated in full three times, corresponding to the three pulses of sound seen in the spectrogram. Overall, during each cycle the wrist moves in a circular motion, moving caudoventrally, then laterally, then craniodorsally, and finally medially back to the starting position. The tail is fanned and elevated as the primary tips slide past in the opposite direction (Fig. 5A,B,2–4) and it relaxes back to its relatively ventral position while the wings are recovered to their dorsal position (Fig. 5A,B,6–8). The head, neck, and the breast are raised and stretched upwards and then back to a resting position in one smooth continuous motion made during the three wing rubs.

This kinematic mechanism does not fit the predictions of any of the four previously hypothesized mechanisms, and thus represents a new class of kinematic mechanisms: wing and tail feather interaction/rub. Physically, the *rub-snap* may be created by any of the three proposed mechanisms as follows: (1) by primary-against-tail feather collisions (percussion), (2) by collisions among adjacent flight feathers elastically loaded by tail resistance (percussion), or (3) through a rapid flick of

the elastically loaded tips of the primaries into the air (sonic-boom or collapsing vacuum mechanisms). The first hypothesis is weakest because the tail and wings are not clapped or beat together in any forceful way, as would be expected for a sound made by percussion; rather, they appear to slide past one another. The video footage also shows that individual wing feathers bend, separate from, and then rejoin each other as the wings slides past the tail in a way that is more consistent with the second and third hypotheses. Specifically, as the feathers slip past the tail, successive feather vanes or rachii may clap against each other to produce sound, or alternatively whip rapidly into the air.

Claps: *Pipra mentalis*

Together a series of *claps* create an explosive, *tack! tack! tack!* sound, like a toy machine-gun. *Claps* were given in series of 3–10 in a row (6.38 ± 2.45 ; $N=8$). Acoustically, each ‘tack’ or ‘clap’ is actually two distinct and brief broad-frequency pulses in quick succession. The two pulses are not identical; the first is relatively low-amplitude, and its range of frequencies higher; the second is louder, more abrupt, and of a lower range of frequencies than the first pulse (Fig. 1). The dominant frequency of the first and second pulses are 4.48 ± 1.28 kHz (2.89–7.12 kHz; $N=8$) and 3.90 ± 0.63 kHz (2.76–4.80 kHz; $N=8$), respectively. The two pulses within a *clap* are separated by 22.17 ± 0.76 ms (20.97–23.36 ms; $N=8$), and the interval between consecutive *claps* is 185.01 ± 10.37 ms (170.84–201.48 ms; $N=8$).

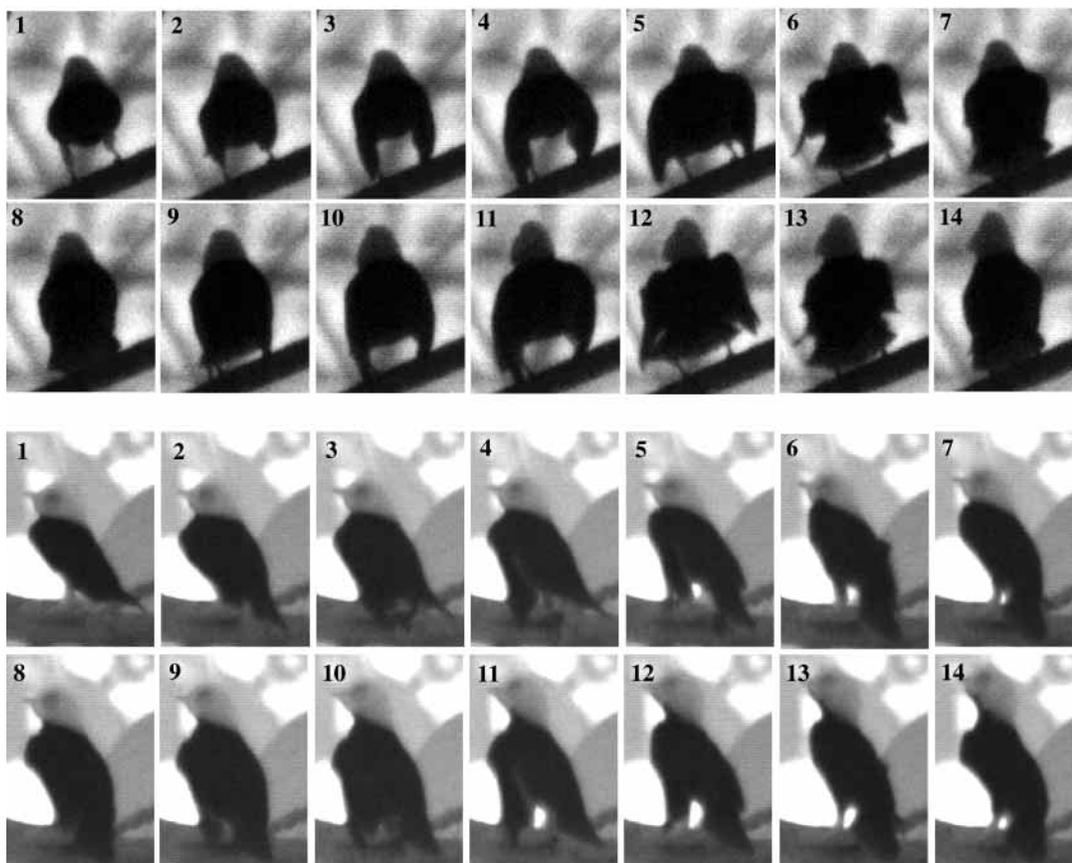


Fig. 5. Posterior and lateral views of *Pipra mentalis* producing a *rub-snap*. Two of three cycles are shown. Intervals between frames are 2 ms. Sound production is hypothesized to occur between frames 5 and 6 and 11 and 12.

While perched in a stereotypic head-down, tail-raised posture, each double-pulsed *clap* is made by two movements: (1) a wing flick into the air (Fig. 6.7) followed by (2) a forceful clap of the wings against the sides of the body (Fig. 6.13–14, $N=24$ high-speed recordings). First, the perched male raises his wings above his back as if he was going to make a normal propulsive wing-beat (Fig. 6.1–6). The first of the two pulses of sound is made by a rustle or flick of the partially open wings before the downstroke begins. This flick is executed by first raising the posterior edge of the wing to about a 45° angle above the body while opening the wrist and elbow joints slightly. The wing is then elevated a few degrees more before a subtle pronation motion initiates the downstroke (Fig. 6.7). The timing of the elevation–pronation transition corresponds to the production of the first sound pulse, and a wave or rustling of the secondary feathers is visible (Fig. 6.7). Subsequent to the wing flick, the second sound pulse is made by the collision of the wings against the body. The opened elevated wings are pulled downward through the air, with the primary feathers bending backward from air resistance (Fig. 6.8–10). When the wings are fully extended laterally, the male flexes the elbow and wrist joints, forcefully closing and adducting the wings against his body (Fig. 6.10–12). The thigh in particular reverberates with the impact of the wing, coincident with the production of the second pulse of sound (Fig. 6.14). This act effectively returns the wing to its resting position. The bird stands motionless, still leaning forward over the perch, often with the tail vibrating slightly, before opening the wings again, ~ 180 ms later, to make the next *clap*.

Kinematically, the motions observed in the first pulse are consistent with the wing-flick into the air hypothesis, and motions observed to produce the second pulse are consistent with the wing-to-body hypothesis; thus, two previously proposed kinematic mechanisms are used to produce this one sonation. As with the *click* and *rub-snap*, we cannot reject any physical hypothesis on how the first pulse is made: either collisions between adjacent secondary feather rachii, or by creation of a low-pressure center behind the wing as it is flicked slightly upward before the downstroke. The second pulse,

however, corresponds with a percussive event after which there is no wing motion, which precludes the non-percussive hypotheses, thus this sound appears to be made by the percussion of the ventral wing surface against the body.

Non-snap sonations

Snort: Manacus

The wing *snort* is a low flatulent sound. Acoustically, it is a series of relatively soft, brief, rapidly repeated, low-frequency pulses (Fig. 7). The number of pulses comprising a *snort* is 10.22 ± 1.20 pulses (8–13 pulses; $N=23$). Intervals between pulses are 12.44 ± 0.98 ms (10.02–13.51 ms; $N=22$). Peak pulse frequency is 2.25 ± 0.44 kHz (1.53–2.98 kHz; $N=23$).

The wing *snort* is produced by a series of rapid lateral flicks of the primary feathers, made by a modified wing-beat as the male springs nearly vertically from the cleared ground of his court to the top of one of the vertical saplings bordering the court (Fig. 8, $N=13$ high-speed recordings). As the male rises from the ground, he flicks the manus and primaries laterally in a rapid extension/flexion motion of the wrist and elbow joints (Fig. 8.4,7,10). Analysis of numerous recordings indicate these sound-producing wing-beats are shallow, with an arc or excursion of only about 60° . The intervals between successive wing flicks are extremely short (12.44 ± 0.98 ms), such that the wings cycle twice as fast as in normal propulsive flight (27.14 ± 2.4 ms; $N=21$). Each wing stroke corresponds to one pulse of sound, thus we hypothesize that the sounds are physically produced by the rapid motion of the primary feathers through the air, an action which may briefly induce vibrations in the feathers. Males were occasionally observed to produce this sound while perched.

Rattle: Manacus

Wing *rattles* sound like low nasal snickers. *M. manacus* only *rattled* infrequently, therefore no acoustic recordings were made, and measurements are from *M. candei* and *M. aurantiacus* only. Acoustically, rattles are 1–3 (2.09 ± 0.73 ; $N=23$) brief, soft, low-frequency pulses (Fig. 7). Pulse intervals differed significantly between *M. candei* and *M.*

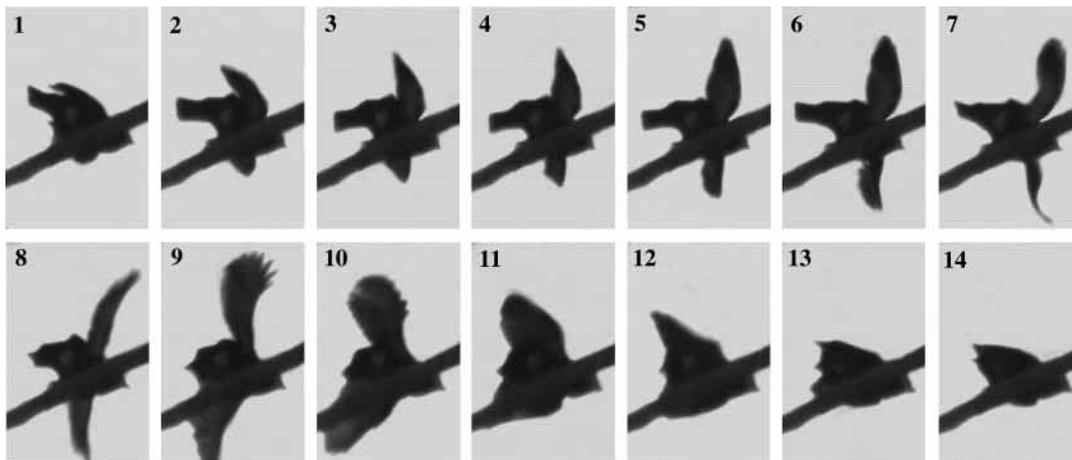
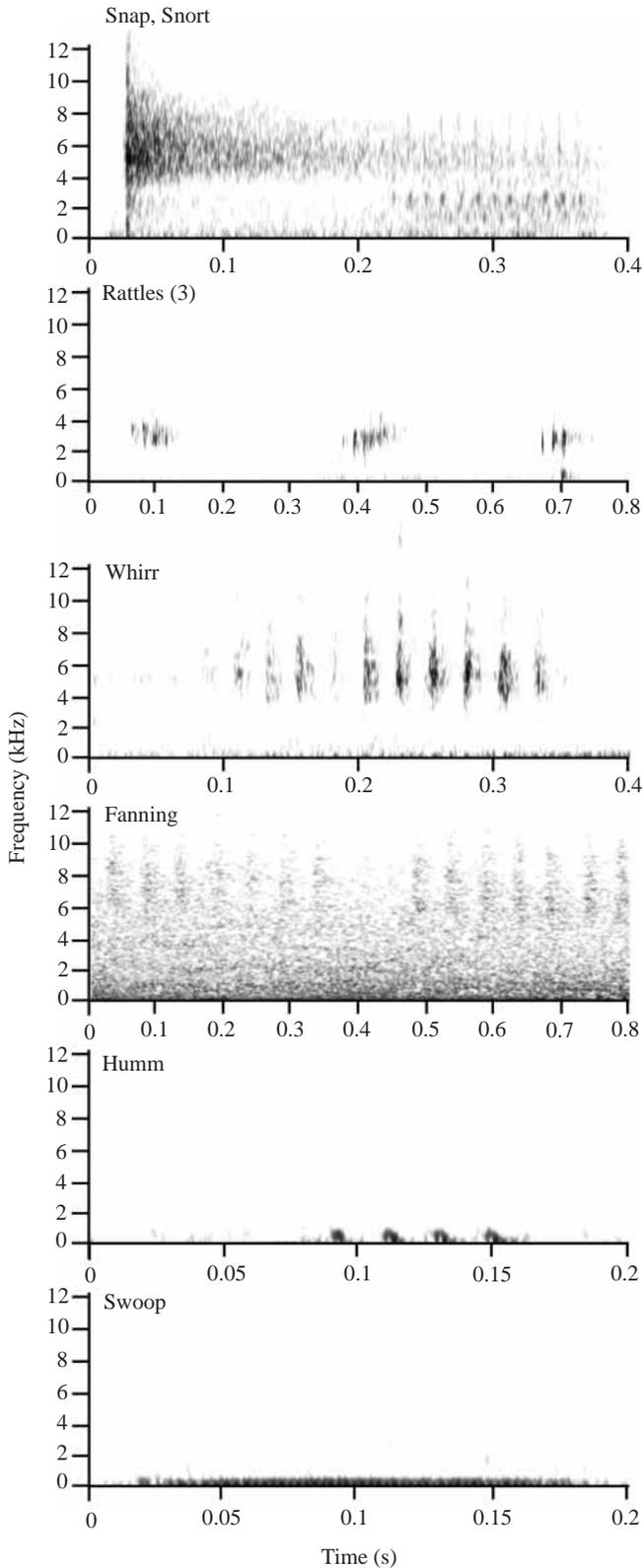


Fig. 6. *Pipra mentalis* producing one *clap*. Vento-lateral view; the male's head is lowered to the left, and his tail is up and pointing right. Intervals between frames are 4 ms. Production of the 1st and 2nd pulses of sound occur on frames 7 and 13, respectively.

aurantiacus: 15.57 ± 0.86 ms (14.1–16.5 ms; $N=10$) for *M. candei*, and 20.29 ± 1.13 ms (18.3–22.1 ms; $N=7$) for *M. aurantiacus*. The peak pulse frequency of 2.38 ± 0.27 kHz (1.46–2.84 kHz; $N=23$) did not differ between species.



Production of *rattles* was not captured on high-speed video; these sounds are produced sporadically during short flights around the male's territories, often moments before descending to the display court (K.S.B., personal observation). Acoustically, the peak frequencies of *rattles* overlap with those of *snorts*. We hypothesize that the same basic kinematic and physical mechanisms are used to generate the sound; modified wing-beats in the form of rapid lateral flicks may be used to induce resonant vibrations in modified primary feathers. Differences in the intervals between pulses in *snorts* and *rattles* may be due to the different behavioral contexts in which they are produced, the former made during courtship in a short (>1 m) vertical ascent from the forest floor, and the latter during level flight around the territory.

Whirr: Manacus

Wing *whirrs* are light reedy *whirring* sounds that are frequently produced during normal propulsive flight, and may not be voluntary. Acoustically, they are a rapid series of very low-amplitude, brief, relatively broad frequency pulses of sound (Fig. 7). Peak frequency could not be characterized. Pulse numbers are highly variable, 9.04 ± 4.1 (4–21; $N=23$). This is probably due to the variable number of wing-beats needed for varying lengths of flight. Intervals between pulses are 26.63 ± 1.5 (23.61–29.93; $N=21$), which is not significantly different from independently measured wing-beat intervals measured from high-speed video ($250\text{--}1000$ frames s^{-1}) of flying birds, 27.14 ± 2.4 ms (24–32 ms; $N=21$), ($P=0.47$, $t=-0.73$, $d.f.=33$).

Kinematics used for production of this sound were not distinguishably different from normal flight motions captured on high-speed video. We hypothesize that these sounds are also made by the modified primaries when moved through the air in normal propulsive flight. However, the rate of airflow and/or the positioning of the feathers may not induce the same resonant vibrations that produce the more tonal *snort* and *rattle* sounds, and may be due to friction or non-resonant feather vibration. The degree to which this sound can be intentionally modulated is not known.

Fanning: Manacus

Fanning sounds like a persistent reedy rustling. Acoustically it is a rapidly delivered series of very low-amplitude, brief, broad-frequency pulses (Fig. 7). Peak frequency could not be adequately characterized. Intervals between pulses are 52.44 ± 2.13 ms (47.90–55.57 ms; $N=9$), two to four times slower than other mechanical sounds produced by *Manacus*. Males assume *fanning* behavior and

Fig. 7. Spectrograms of six non-snap sonations*. From top to bottom as labeled: a *snap* and subsequent twelve-pulsed *snort* (*M. manacus*); three multi-pulsed *rattles* (*M. aurantiacus*); a sample of *whirring* (*M. manacus*); a sample of *fanning* (*M. manacus*); four *hum* pulses (*P. mentalis*); the extremely low-frequency *swoop* (*P. mentalis*). Detailed descriptions of motions are given in text. *Note variation in time-axis scale among spectrograms.

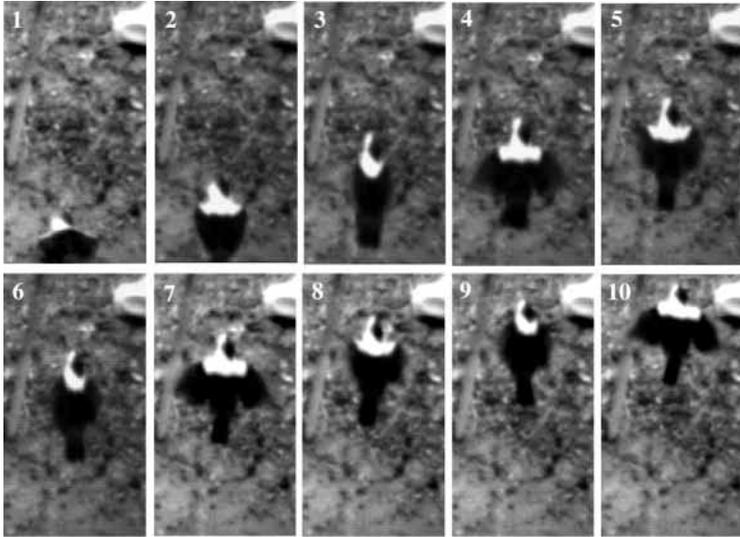


Fig. 8. Dorsal view of *M. manacus* producing a *snort*. The male is crouched on the floor of his court in frame 1, and airborne between frames 3–10. The display perch is in the upper left. Three sound pulses shown, produced during frames 4, 7, and 10. Intervals between frames are 4 ms.

can continue for several minutes at a time, such that the number of pulses is highly variable.

This sound is produced by continuous lateral flicks of the primary feathers of a perched male made at a rate four times slower than *snorts* ($N=2$ high-speed recordings). The male assumes a crouching position, so that his legs are not visible beneath his body, which is low and horizontal (Fig. 9.1). The male rotates his humerus, apparently to orient the wing into the correct posture for lateral opening. He extends the elbow and wrist joints, such that the wing surface opens out laterally, and the primaries are flicked outward (Fig. 9.2). The wing is slightly depressed as the elbow and wrist joints are flexed, closing the wing in to a resting position (Fig. 9.2,3), from which the cycle begins again.

We hypothesize that *fanning* is made either by movement of air over modified primaries, or by the friction of flight feathers brushing across one another. The speed and position of the feathers as they move through the air do not appear to generate the resonant vibrations that produce the *snorts* and *rattles*. Nonetheless, this sound is clearly modulated and intentionally produced.

Fanning was reported in *Manacus manacus* by Snow (1962), and was only observed in *Manacus manacus* in this study.

Humm: Pipra mentalis

The sound is a low *hum*, reminiscent of that of a hummingbird in flight, but deeper. Acoustically, it is a series of 2–5 (4.20 ± 0.89 ; $N=20$) low-frequency pulses (Fig. 7). Intervals between pulses were 21.11 ± 2.02 ms (18.80 – 24.50 ms; $N=20$). Peak pulse frequency was 184.0 ± 157.2 Hz (20.0 – 520.0 Hz; $N=20$), with high frequency measures of 982.0 ± 52.7 Hz (880.0 – 1090.0 Hz; $N=20$). The average duration of a single low-frequency pulse was 6.50 ± 0.91 ms (5.05 – 8.32 ms; $N=20$).

This sound is made in flight by the wing feathers as they move through the air during propulsive downstrokes shortly after the bird leaves its perch. How the wing kinematics used to produce the *hum* differ from that of normal propulsive flight was not determined. *Humms* are made in the first few (2–5) strokes of flight following a *click* and departure from a perch. Intervals between *hum* pulses are identical to intervals between successive flight strokes. It seems likely that *humms*



Fig. 9. Dorso-lateral view of wing motions used during *fanning* of *M. manacus*.

are made when the feathers are moved through the air at a speed and posture that induces resonant vibrations.

Swoop: Pipra mentalis

The *swoop* is a subtle sound that is easily missed. It sounds like a heavy object bounced once on a large rubber membrane, a soft gulping sound, or a pluck on a contrabass string. Acoustically, it is relatively long in duration 162.60 ± 17.46 ms (119.60 – 178.20 ms; $N=12$), with a peak frequency always measuring between 1 and 20 Hz ($N=12$) and a maximum frequency of 664.2 ± 68.9 Hz (510.0 – 750.0 Hz; $N=12$) (Fig. 7).

The sound is made when the male, flying at extremely high speeds, dives precipitously in his flight trajectory, swooping toward the ground ($N=22$ conventional video recordings). Beyond this, the kinematics of sound production cannot be described in detail because production of this sound was not adequately captured on high-speed video. The *swoop* is acoustically similar to *humms*, and is probably produced by a similar physical mechanism. However, while *humms* are made when the wing is moved rapidly through the air during propulsive flight strokes, the *swoop* is most likely made as the whole wing is simply held opened at a critical moment when the rapid movement of the bird's body through the air can induce the vibrations necessary to produce the sound.

Discussion

This research provides the first detailed examination of the competing hypotheses describing the kinematics of wing sonation in birds. Rather than uncovering which one of four competing mechanisms birds use to produce *snap* sounds with wings, each of four distinct kinematic mechanisms are verified. Additionally, a diversity of non-*snap* sonations are described whose kinematics are distinct from those of *snap* sonations. These results also highlight numerous unusual aspects of piprid biology. Extreme rates of muscle contraction are documented in both of the clades examined, inferred from the extremely rapid wing cycles used in sound production. The kinematic descriptions provide a functional context in which to place the unusual aspects of morphology found in *Manacus*. Finally, and most significantly for the fields of communication and macroevolution, an unanticipated degree of acoustic, behavioral and mechanistic diversity is uncovered in this previously poorly studied mode of communication. Thus, what have previously been classified by ornithologists as 'manakin wing sounds' are shown to be 11 acoustically and behaviorally distinct sonations, with *Manacus* employing at least two fundamentally different kinematic mechanisms of sound production, and *Pipra mentalis* using at least four kinematic mechanisms, at least three of which do not overlap with those of *Manacus*.

Kinematic and physical mechanisms

The two basic acoustic classes of sonation known from other birds are found in both clades of piprid studied. The first class of sounds, wing-*snaps*, are made using three of four previously

hypothesized kinematic mechanisms: (1) clapping the dorsal surfaces of the wings together above the back (*snap* and *roll-snap* of *Manacus*), (2) clapping the ventral surface of the wings to the body (*clap* 2nd pulse of *P. mentalis*), and (3) rapidly flicking wing feathers into the air (*click* and *clap* 1st pulse of *P. mentalis*). A fourth, previously unproposed mechanism of rubbing the primary feathers against the tail feathers (*rub-snap* of *P. mentalis*) is discovered. This multiplicity of kinematic mechanisms was not predicted and highlights how poorly known these communicative signals are in birds.

The second class of sounds, the lower-amplitude and often lower-frequency, pulsed or sustained notes, are made by both *Manacus* (*snorts*, *whirrs*, *rattles* and *fanning*) and *Pipra mentalis* (*humms* and *swoops*). Most of these sounds are made using the basic kinematic motions of cyclical wing movements (the *swoop* excepted), mostly during flight (*fanning* excepted), but how these motions differ from normal, silent flight is not clear. At least *snorts* and *fanning* seem to emphasize a lateral extension/flexion motion of the elbow and wrist joints. That these sonations vary in the number, rate, and acoustic structure of pulses, may indicate the physical mechanisms involved in making these sounds may not be identical among them. That is, the wings may cycle regularly to produce sounds, but some cycling may induce resonant vibrations in primary feathers, while others may simply result in friction among adjacent flight feathers. More research is required to distinguish between these possibilities.

Our kinematic data describe the gross, body-level motions used to produce the class of *snap* sonations, thus allowing us to generate preliminary hypotheses at the finer level of the physical mechanisms involved in *snap* production. For most of the described sonations it is impossible to distinguish without further research which of three physical mechanisms: (1) percussion, (2) sonic-boom or (3) collapsed low-pressure center, are used to sonate in these two clades. Gross-level percussion (wings against wings or wing against body) is the kinematic and physical mechanism most likely to be used by *Manacus* in its *snaps* and *rolls*, and by *P. mentalis* in its *claps* (2nd pulse). Feather percussions among a suite of adjacent feathers may produce the *rub-snaps*, *clicks* and *claps* (1st pulse) of *P. mentalis*, or alternatively, any or all of these sounds may be produced by air-compression/expansion events or a miniature sonic boom caused by the rapid whip-like movement of the whole wing. As regards the non-*snap* sonations, induced vibrations of primary feathers may be involved in the production of *snorts*, *whirrs*, *rattles* and *fanning* of *Manacus*, and the *swoops* and *humms* of *P. mentalis*. Alternatively, we propose that friction created when feathers move over one another may also create these sounds, and is particularly likely to explain the broader-frequency, less tonal sonations, such as *fanning* and *whirr* in *Manacus*.

Morphological and physiological significance

Motor requirements for sound production in manakins have pushed them to physiological extremes. If we can assume that the repeated, sequential contractions of individual wing

muscles are responsible for the repeated, sequential or cyclical wing movements that we recorded, then given that these wing cycles relate in a one-to-one manner with the sound pulses they produce, the inter-pulse intervals of the sounds that we measured should accurately represent the rates of muscle contraction used to produce these sounds. Thus, wing cycle frequencies used to produce *roll-snaps* and *snorts* in *Manacus* and *rub-snaps* in *P. mentalis* are comparable to those used by hummingbirds for flight (Mason-Barr and Pye, 1985; Lasiewski and Lasiewski, 1967; Calder and Calder, 1992). These results thus provide independent support for the premise that ‘sonic muscles’, those used in sound production, are among the fastest vertebrate muscles known. Specifically, the shaker muscles of a rattlesnake’s rattle contract at ~90 Hz, several times faster than more normal vertebrate locomotory muscles, which contract at 20–30 Hz (Rome et al., 1996). The piprids described herein can employ similarly rapid wing cycles of 75 Hz (*P. mentalis*, *rub-snap*) and 80 Hz (*Manacus*, *snort*), at least doubling the contraction rates used in normal flight.

Previous morphological work has uncovered striking modifications of the wing morphology of *Manacus* (Lowe, 1942; Schultz et al., 2001; Bostwick, 2002; K.S.B., unpublished data) and other species in the Pipridae, including *P. mentalis* (Bostwick, 2002; K.S.B., unpublished data). The wing kinematics described above provide a preliminary functional context in which to interpret the morphological modifications found in *Manacus*, but they also complicate morphological interpretation by showing that the *snaps* and *rolls* of *Manacus* are produced by fundamentally different wing kinematics than *snorts* and *fanning* (and presumably *whirrs* and *rattles*). Thus, we now know that any given morphological modification needs to be examined not only as a potential modification for sonation in general, but as a modification for one of several particular sonations. Fortunately, the four *Manacus* sonations captured on video are probably the most functionally important ones (Chapman, 1935; Snow, 1962), and each employs only one of two fundamentally different sound-generating motions; the explosively loud *snaps* and *rolls* are produced by a medially oriented clap of the dorsal wing surface, while *snorts* and *fanning* are produced by a series of extremely rapid, lateral wing flicks.

The *snaps* and *roll-snaps* are produced by forceful adduction of the dorsal wing surface, as opposed to forceful depression of the ventral wing surface, and thus involve generation of force in the direction opposite that required for flight. The primary motion used to create the medial clap appears to be supination and retraction of the humerus, while the flexion of the wrist and elbow joints remains open and constant. We therefore predict that those muscles whose primary action involves retraction and/or supination of the humerus are largely responsible for the production of *snaps* and *roll-snaps*. Two of the three largest flight muscles, the scapulohumeralis caudalis and the supracoracoideus, retract the humerus; the former also pronates, while the latter supinates (Raikow, 1985). Together

with the primary downstroke muscle, the pectoralis, these muscles have been quantitatively compared in terms of mass and physiology between male and female *Manacus vitellinus* and *Taenopygia guttata* (Zebra finch). Male *M. vitellinus* exhibit muscular modifications in males relative to females, and in *M. vitellinus* relative to the control species (Schultz et al., 2001). The scapulohumeralis caudalis in particular exhibits the greatest disparity in mass and fiber type composition (Schultz et al., 2001), and in a manner consistent with those expected for increased force generation and muscle contraction speeds. While consistent with our predictions, this interspecific comparison (Schultz et al., 2001) was made between *M. vitellinus* and *T. guttata*, of which the former were wild-caught, and the latter were captive individuals of a distantly related, ecologically distinct species that does not perform physical courtship displays. Thus, the great differences between the comparative and control species allows for numerous alternative explanations for the morphological differences found.

Additional support for our premise that observed modifications of male *Manacus* shoulder myology, and the scapulohumeralis caudalis and the supracoracoideus in particular, can be attributed to their use in adducting/retracting the wing during *snap* production, is provided by myological comparisons of *M. manacus* with other, wild-caught, territorial manakin species that also perform physical displays but do not wing-snap (Bostwick, 2002; K.S.B., unpublished data). Such comparisons reveal that, in general, sonating piprids have distinctive and localized morphological modifications relative to non-sonating ones. Relative to non-sonating piprids, *Manacus* in particular exhibits an exceptionally hypertrophied scapulohumeralis caudalis, a moderately hypertrophied supracoracoideus, a modified humeral head (that partially determines the mobility of the shoulder joint), and a scapula with a uniquely widened blade among piprids (a modification that presumably accommodates the hypertrophied scapulohumeralis caudalis; Bostwick, 2002).

There is anatomical and experimental evidence that the scapulohumeralis caudalis retracts the humerus (Raikow, 1985; Dial, 1992). Wing-propelled divers such as penguins, which generate force during both the downstroke and upstroke of the wing, have greatly enlarged scapulohumeralis caudalis muscles, indicating that this muscle is indeed important for generation of force in a dorsal/medial direction (Dial, 1992). Thus, the understood role of the scapulohumeralis caudalis in humeral retraction, the primary motion involved in creating the medial wing clap, makes its potential role in sound production in general, and the *snap* and *roll-snap* sonations specifically, extremely plausible. Further, the moderately hypertrophied supracoracoideus probably aids in the humeral retraction and adds the element of humeral supination observed, bringing the leading/anterior edges of the wing into forceful contact.

In contrast to the *snap*-generating medial clap, in which the elbow and wrist joints are held relatively fixed, the *snort* and *fanning* sonations entail rapid lateral flicks executed by repeated flexion/extension motions of the elbow and wrist

joints. Numerous muscles in the forewing of *Manacus* are hypertrophied, the most notable being the elbow and wrist joint extensors, such as the humerotriceps and the extensor metacarpi radialis, and the flight feather flexors, such as the flexor carpi ulnaris cranialis and caudalis (Bostwick, 2002). Additional modifications of the forewing that are likely to relate to the production of *snorts* include the extremely shortened carpometacarpus of the manus (Bostwick, 2002), which may promote rapid wing-flicking, and the deeply incised, decurved and reduced primary feathers unique to *Manacus* among manakins (Chapman, 1935). Incised primary or tail feathers are common in species known to sonate in flight display dives (Miller, 1925; Pettingill, 1936; Carr-Lewty, 1943; Tuck, 1972; Craig, 1984; Miskelly, 1990). Such feather modifications are hypothesized to be an adaptation to enable the feathers to vibrate more readily when air is forced through them at the high speeds reached in dives.

Thus, the morphological modifications unique to *Manacus* are consistent with those expected to execute the sound-producing motions observed on video. The distinct kinematics used to produce different sonations appear to have resulted in several equally distinct morphological modifications. These preliminary analyses indicate that more detailed morphological work and kinematic data may very well yield a relatively sophisticated understanding of this unique functional-morphological system in *Manacus*.

Evolutionary and behavioral significance

Perhaps the most outstanding feature of this system is the diversity of sonations represented by these two clades, and the multiple means by which that diversity has been achieved. Thus, the two clades use largely non-overlapping kinematics to produce sounds, both clades use more than one kinematic mechanism, and at least *Manacus* also employs the same mechanism in different behaviors to increase repertoire size. For instance, *Manacus* uses the same kinematics, claps of the dorsal wing surface, in a single airborne clap to produce the *snap*, and also while perched in a repeated train of claps to create the *roll-snap*. Meanwhile, *P. mentalis* increases its repertoire by employing a multiplicity of kinematic mechanisms, creating its *snaps* in three distinct ways.

While this research uncovers unanticipated levels of diversity, these observations are restricted to only two of as many as five phylogenetically independent sonating clades, and only four of approximately 20 sonating manakin species. Sonations made by members of other piprid genera *Corapipo*, *Ilicura*, and *Heterocercus* may be independently evolved, and are behaviorally and acoustically distinct from those reported here. Existing information indicates that these clades are likely to use kinematics and/or physical mechanisms of sound production distinct from those described here (Prum, 1998).

The acoustic, behavioral, mechanistic and morphological diversity surrounding sonation raises the question of what evolutionary forces may underlie such rampant character evolution. The role of sonations in courtship displays supports the hypothesis that piprid wing sounds have evolved by female

choice. Across aves, and in piprids in particular, the origin of sonation is associated with female choice (Prum, 1998). Thus, the diverse acoustics, kinematics, morphology and behaviors involved in piprid sonations document a sexually selected character radiation. Subsequent to the multiple origins of sonation in the family, sexual selection has fostered an explosive diversification in all aspects of biology relating to non-vocal wing sound production.

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