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S01-1　Mechanisms of feather sonation in Aves: unanticipated levels of diversity

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Abstract Sonations, intentionally modulated acoustic signals produced by nonvocal structures, are poorly studied in birds and little is known about the diversity of mechanisms used. Here I review feather-produced sonations and proposed sound-production mechanisms, with particular emphasis on sounds produced by wings. I then summarize the results of my own research on mechanisms of sonation in the Neotropical manakins (Pipridae). This research demonstrates for the first time how various *snap* sonations are produced, and shows that many mechanisms can be used to generate acoustically similar sounds.

Key words Acoustic communication, Mechanical sounds, Pipridae, Sonations, Wing sounds, High-speed video

1 Introduction

Although birds are renowned for their voices, many species also communicate acoustically by nonvocal means. Such signals have been termed instrumental music (Darwin, 1871), mechanical sounds (Prum, 1998), and *sonations* (Bostwick and Prum, 2003). The latter term was proposed to emphasize the distinction between nonvocal and vocal signals, and to create a companion verb, to *sonate*, to refer to the act of producing nonvocal acoustic signals. Avian sonations are thus intentionally modulated, communicative sounds produced by non-syringeal structures such as bills, feet, and feathers.

Feather sonations can be difficult to observe under field conditions as they are often produced by extremely rapid movement of small structures during complicated courtship displays, and often at some distance from the observer. Indeed, many of the best-known sonations have been subject to lengthy debate about their nonvocal nature (Bent, 1927; Baptista and Matsui, 1979; Sutton, 1981; Pytte and Ficken, 1994). Consequently, most hypotheses of the mechanics of sound production by feathers are speculative, and the range of physical and kinematic mechanisms used to produce such sounds is largely unknown.

I here provide a brief overview of the diversity of feather-produced sonations, summarize the means by which birds are thought to produce wing-sonations, and then summarize the results of recent research which demonstrates that the mechanisms of sonation are far more diverse than previously thought.

2 Sonating feathers

Birds use nearly every conceivable part of the body to sonate, from bills and feet to feathers and combinations thereof. Mechanisms of bill and foot sonations are relatively easy to infer and commonly involve percussive contact between body parts and/or substrate. Feather sonations are more diverse and widespread, yet most are poorly understood mechanistically. I discuss feather sonations and mechanistic hypotheses by feather types below.

2.1 Conture feathers

High-speed videos of courting in sage grouse (*Centrocercus urophasianus*) have shown that displaying birds rub the manus or wrist feathers against specially stiffened breast feathers to create a *whoosh*-like sound (Dantzker, pers comm.). In this case, the mechanism of sound production is clearly feather-to-feather friction.

2.2 Tail feathers

Two types of tail-generated sounds are produced in different behavioral contexts: *whistles* produced in flight and *rustles* produced while perched. Whistles emanating from birds diving aerially have often been attributed to specialized tail feathers which are thought to vibrate regularly when air flows over them at high speeds (Carr-Lewty, 1943; Thonen, 1969; Reddig, 1981; Sutton, 1981). This interpretation has been supported by artificial manipulation of feathers. Even so, it needs to be treated with caution for, although manipulation of isolated tail feathers of Anna'a hummingbird (*Colypte anna*) produced sounds similar to the flight sound given at the bottom of its dynamic display (Rogers, 1940), Baptista and Matsui (1979) demonstrated that a vocalization given by the bird when perched was spectrographically identical and argued that such sounds produced in the dynamic display could be syringeal in origin. Several species of snipe (*Gallinago*, and *Coenocorypha*), nevertheless, do produce whistling sonations with specialized tail feathers (Sutton, 1981; Miskelly, 1990), as do hummingbirds (Wells and Baptista, 1979), honeyguides (Mackworth-Praed and Grant, 1957) and manakins (Prum et al., 1996).

Tail rustles, in contrast, have been described primarily from the ground-based courtship displays of male grouse (Johnsgard, 1983). The physical mechanisms of sound production behind tail rustles and rattles in such circumstances are unknown, but probably involve friction and/or percussion.

2.3 Wing feathers

In birds, the wing is by far the most frequently used vehicle for sonation. Passeriformes (Payne, 1973; Craig, 1984; Manson-Barr and Pye, 1985; Zimmerman et al., 1996; Prum, 1998), Piciformes (Raffaele et al., 1998), Caprimulgiformes (Miller, 1925), Apodiformes (Miller and Inouye, 1983; Calder and Calder, 1992), Charadriiformes (Pettingill, 1936), and Galliformes (Johnsgard, 1983) all contain members known to produce prominent and intentionally modulated wing-sounds. Scores of other birds produce wing-sounds of lesser strength and prominence, and less clear modulation. Morphological modifications such as attenuated primary feathers are associated with sonations produced in flight, and are described frequently in the literature. As in tail sonations, *whistles* produced during flight are common; and *rustles*, produced both in flight and when perched, are known too. There is, as well, an additional category of sounds that is acoustically and, presumably, mechanistically different. These are often called *claps* or *snaps*.

3 Categories of wing sounds

There are three basic wing-produced sonations, classified by the quality or acoustic structure of the sound produced. Acoustic structure has as yet undetermined connections with sonation mechanisms. For the sake of simplicity, I refer here to these three general classes of wing sonations as *whistles*, *rustles* and *snaps*.

3.1 Whistles

Whistles, comprising a variety of pulsed and tonal sounds produced in flight, are often described as chirps, whirrs, whistles, winnows, and roars. Analogous to tail whistles, such sounds are universally attributed to vibrations caused when air is forced through flight feathers (Miller, 1925; Pettingill, 1936; Tuck, 1972; Craig, 1984; Miskelly, 1990). It is further hypothesized that the pulsing nature of some of these sounds corresponds to wing-beat cycles. Miller and Inouye (1983) glued together modified primaries implicated in the flight whistle of the broad-tailed hummingbird (*Selasphorus platycercus*) and succeeded in silencing the sound, which was subsequently restored when the glue was removed. Several researchers have found that modified feathers can be induced to vibrate experimentally at frequencies overlapping those of sounds given in nature (Carr-Lewty, 1943; Reddig, 1978). Thus, air-induced vibration of feathers seems the most conceivable means of sound production in the wing, with the caveat that syringeal sources must be eliminated before such a cause is accepted in each case.

3.2 Rustles

I suspect that rustles will ultimately be shown to be caused by feather-to-feather friction during flight. For example, Stephanie's bird of paradise (*Astrapia stephaniae*) produces a loud rustling *buzz* during flight (Frith and Beehler, 1998), which can be produced by just one flap of the wing (E. Scholes, pers. comm.). In this species, unusually pointed, curved, and thickened barbs are developed along the leading edges of otherwise normal primary feathers (Bostwick and Scholes, pers. obs.).

3.3 Snaps

Such sounds comprise brief, usually loud or sharp, broad-frequency (toneless) notes, often referred to as *clicks*, *snaps*, *pops*, or *claps*. When describing such sonations, authors rarely speculate on how they are produced beyond implicating the wings (Payne, 1973; Bomford, 1986; Sankaran, 1996). Bertram (1977) nevertheless suggested that the flight "claps" of *Mirafra* larks are made either by striking adjacent wing feathers together or by an abrupt interruption of the airflow between wing flaps; but evidence that would shed further light has not been forth coming.

4 Mechanisms of *SNAP* sonations in Pipridae

4.1 Results of prior studies

Sonations reach the zenith of their use in the Neotropical manakins, family Pipridae. Males of over half of the species of manakins incorporate such sounds into their elaborate courtship displays; and many have repertoires that include more than one behaviorally and acoustically distinct sonation. Phylogenetic relationships in the Pipridae indicate that many of the sonations have arisen independently of one another (Prum, 1998; Bostwick, 2000). The genus *Manacus* is perhaps best known for its gratingly loud sonations. At least six behaviorally or acoustically distinct sounds have been described from its members (Chapman, 1935; Skutch, 1969; Snow, 1962a). Two of the most striking, the *snap* and *roll-snap*, are also the most frequently used, and fall into the category of wing-snap sonations.

Many authors have proposed mechanisms for sonations in *Manacus*; and most agree that modified secondary feathers are involved in producing the *snap* and *roll-snap* (Chapman, 1935; Sick, 1959; Snow, 1962a; Skutch, 1969; Prum, 1998). Chapman (1935) and Stolzmann (1884) attributed *snaps* and *roll-snaps* to the striking together of adjacent secondary rachii within a wing, such that opposite wings do not contact one another. Snow (1962b) suspected that the wings are rapidly "vibrated," so that the secondaries brush "against one another rapidly as the wing is opened and closed." Skutch (1969) described the wings as being lifted above the bird's back and "beat(en)". Prum (1998) thought that the wing feathers were clapped against the body. Both Prum (1998) and Skutch (1969) concluded that *roll-snap*s arose from repetition of the motions used to produce single *snap*s.

Like the species of *Manacus*, *Pipra mentalis* (red-capped manakin) also sonates. Skutch (1949, 1969) described two sonations in this species: *snaps* made while perched, and *rustles/whirrs* produced in flight. He found that *snaps* were used in three different behavioral contexts, and that the rate of snap production varied according to the context. Thus there was a single, simple snap given before flight, a rapid *whirring snap* made periodically after alighting on a perch, and more slowly-delivered snaps produced by the male "while resting". All of these behaviorally distinct snaps have since been considered variations of a single basic sonation, called the "*klok*", in this and other species of *Pipra* (Snow, 1963, 1977; Schwartz and Snow, 1978; Robbins, 1983; Tello, 2001).

In descriptions similar to those of Chapman (1935) for *Manacus*, Skutch (1969) attributed the snaps of *Pipra* to "rapid movements of the wings causing the thick shafts of the plumes to strike noisily together." Prum (1998) also suggested that *Pipra* uses the same mechanism as *Manacus* to snap, clapping wings feathers against the body. Prum's (1998) acoustic analysis revealed the occasional presence of two sound pulses in extremely rapid sequence as well; these he attributed to the staggered percussion of right and left wings against the body.

4.2 Results of new research

Recent advances in high-speed video technology now make it possible to record birds sonating in field conditions. I used a high-speed video camera at recording rates of 500 and 1 000 frames/second to document sonation in *Manacus manacus* (white-bearded manakin), *M. candei* (white-collared manakin), *M. aurantiacus* (orange-collared manakin), and *Pipra mentalis* (red-capped manakin) at either San Diego Zoo and Wild Animal Park or La Selva Reserve and Carara National Park in Costa Rica. The recordings show that eleven distinct sonations are produced among the species of *Manacus* and *Pipra mentalis*. Five of these, the *snap* and *roll-snap* of *Manacus*, and the three behaviorally distinct snaps of *Pipra mentalis*, now named the *click*, *rub-snap* and *clap*, fall into the *snap* category of wing sonations (Bostwick and Prum, 2003).

The results of this research provide the first mechanistic data to explain how manakins wing-snap, and show that *Manacus* and *Pipra* use diverse kinematic methods to produce such sonations. Members of *Manacus* produce the *snap* and *roll-snap* by clapping the dorsal surfaces of the wings together in the region of the bird's wrists. Single *snaps* are produced while the bird is flying between saplings on its display court, and the *roll-snaps* are produced by cyclic repetitions of the snap-clapping motion while the bird is perched (Bostwick and Prum, 2003). Surprisingly, *Pipra mentalis* does not employ this wing-clapping method to sonate, but instead uses three distinct mechanisms to produce each of its behaviorally distinct snaps. The *clicks* are produced when the wings are flicked out laterally from the bird's sides; the triple-pulsed *rub-snap* is produced when the bird rubs its primaries down the sides of its tail in three cycles of motion; and the double-pulsed *clap*s are produced when the bird first flicks its wings up, producing one pulse, and then claps them down against its thighs, producing the second pulse (Bostwick and Prum, 2003). Thus, not one but nearly every mechanism that previous authors had put forward to account for the wing-snap displays in manakins is in fact used by *Manacus* and *Pipra* in diverse yet stereotyped ways.

5 Conclusions

Luis Baptista expressed a fascination with vocal and nonvocal communication alike. Until recently, however, sonation itself was too diffuse and cryptic a phenomenon in birds to generate much attention. Increased awareness of the phenomenon and new field video technology now allow us to clarify and synthesize the little we know about such sounds and their underlying mechanisms and purpose. This brief summary hints at considerable diversity in feather-generated sonations in birds. They are found in disparate families and orders, and have evidently evolved independently numerous times. Surprisingly, mechanistic diversity has been hiding in even the simplest sounds produced, such as the wing-snaps in manakins. Such diversity highlights the importance of such nonvocal modes of communication in birds, and begs detailed comparative research aimed at exploring the similarities and differences between vocal and nonvocal communication, and their functions.

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