



ADAPTIVE HYPOTHESES ON THE EVOLUTION OF NON-VOCAL COMMUNICATION SOUNDS IN BIRDS

Christopher J. Clark^{1*}

Juan I. Areta²

¹ Evolution, Ecology, and Organismal Biology, University of California - Riverside, USA

² Laboratorio de Ecología, Comportamiento y Sonidos Naturales (ECOSON), Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-CONICET) - Salta, Argentina

ABSTRACT

Birds have evolved to produce communication sounds (sonations) with their wings, tail, feet, or beak dozens if not hundreds of times independently. Ongoing work continues to uncover many new examples of sonations and the physical acoustic mechanisms by which these sounds are produced. The repeated (convergent) evolution of a trait permits sophisticated evolutionary tests of how and why it evolves. Here, we outline a series of adaptive questions about the evolution of sonations: Does producing sonations entail tradeoffs with other functions, such as flight? How do sonations co-evolve with production of vocalizations? How do sonations co-evolve with behavior? Compared to vocalizations, do sonations occupy the same functional space as vocalizations? Do sonations occupy the same acoustic space as vocalizations? Each of these questions has already received some attention within individual bird clades, but with so many independent origins across birds, the bigger picture has only begun to appear.

Keywords: *flight, locomotion-induced sound, mechanical sound, sonation, vocalization*

1. INTRODUCTION

Birds are highly acoustic animals. The ability to vocalize (i.e. produce sounds using airflow through the syrinx, throat, mouth, of the bird) has evolved once. As nearly all major clades of birds and crocodilians vocalize (1), this origin is ancient, and this trait has been lost once: new-

world vultures lack a syrinx making them nearly silent (not-vocal?) (2). Given this nearly uniform presence of the independent variable (vocalizing), it is a challenge to study the origins of vocalizations in birds. Moreover, while many papers study how vocalizations evolve in birds, a common problem is ascertaining homology: functionally similar vocalizations are presumed to be homologous. It is possible that in reality vocalizations evolve quickly such that functional categories such as “songs” might evolve convergently. Simply put, a study that starts by assuming all songs are homologous intrinsically can’t uncover instances of convergence.

These limitations of the study of bird vocalizations are strengths of the study of sonations. Sometimes called “non-vocal” or “mechanical” sounds, sonations are sounds produced by the wings, tail, feet, bill, or other external anatomy, for the purpose of communication (2-4). Recent research has focused on physical mechanism (4-6). Often (but not always: 3), sonations are produced by obviously modified structures. Sonating species such as the Subtropical Doradito (*Pseudocolaptes acutipennis*) may have several modified wing feathers (4). Since feathers are amenable to manipulation (plucking or clipping), it is straightforward to characterize how individual mechanical components each contribute to produce sound. Experiments probing mechanism can make it straightforward to detect when similar sounds are nonetheless not homologous, because their physical origins are clearly different. For instance, some hummingbirds produce nearly identical sounds with the syrinx and the tail (5).

Woodpeckers drum with their beak (10), snipe and hummingbirds make sounds with their tail feathers (6), and birds from doves to flycatchers make sounds with their wings (12-14). Sonations, as a broad collection of non-

*Corresponding author: cclark@ucr.edu

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¹ It is problematic to define something by what it is not. Imagine if vocalizations were called “not-mechanical sounds”.

homologous sounds, have evolved dozens or perhaps hundreds of times in birds. The total number is unknown, as many birds have poorly known natural history, and new examples continue to be uncovered (the two of us have several examples awaiting write-up). As such, questions of how sonations evolve are wide open for study. Here our purpose is to explore a series of adaptive questions that hitherto have been relatively unaddressed in the literature.

2. EVOLUTION

Sonations originate out of adventitious sounds: incidental sounds that arise out of the animal doing something else (7). Once receivers begin to attend to the sound, the sound itself becomes a target of selection. If the sender is rewarded by producing them, the sender *may learn* modifications, or its descendants evolve modifications, and the sound becomes a sonation (7). There are two types of modifications for sound production: modified morphology, and modified behavior. It bears emphasizing: *It is not essential for specialized morphology to evolve for an animal to produce a sonation*. Walruses clap their flippers to produce sound (8) much like humans clap our hands (9), and neither walruses nor humans have known forelimb modifications to make these sounds (but note that whether human clapping is a sonation or not can be debated; human clapping could mean different things to different people, making this a case of a "learned sonation"). Woodpeckers drum to communicate and there are no suggestions their beak morphology has evolved for sound production *per se* (10). The point is: sonations sometimes arise out of modified behavior alone.

That said, the majority of sonations do seem to entail modified morphology, and many entail both modified morphology and modified behavior, such as the wing snap

of manakins (11) or the complex flight display of the Subtropical Doradito (4).

3. QUESTIONS

3.1 Do sonations entail tradeoffs with functions such as flight?

This question is mostly about modified morphology and less so about sonations *per se*. Many sonations are produced by the wings (Figure 1A). Features related to the wingbeat cycle may impose constraints on production of sounds by wings, including at what point during the wing-beat cycle they are produced (4). Feathers modified to produce sound potentially impair flight by affecting the normal aerodynamic forces the feather would otherwise produce during flight. For instance, in Subtropical Doradito, one of the modified feathers (p6) has a broad spatulate shape that cause it to raise during the flight displays in order to let another modified feather (p7) vibrate to produce sound (Figure 1A). While a reduction in the size of p6 might also let p7 sonate, it could impair normal flight, conversely, the broad shape of p6 could allow it to also keep its aerodynamic role during normal flight (4). This tradeoff hypothesis remains largely untested. One line of evidence in favor of the tradeoff hypothesis is widespread: most sonations evolve in the context of sexual signals produced by the male and not the female (12), and virtually all of these species are also sexually dimorphic, where the female does not also have the sound-producing feather morphology. What selects for dimorphism? If the sound-producing morphology were selectively neutral in females, then female morphology should be 'dragged around' by divergent selection on males of different species divergent selection on males of different species. Instead, the

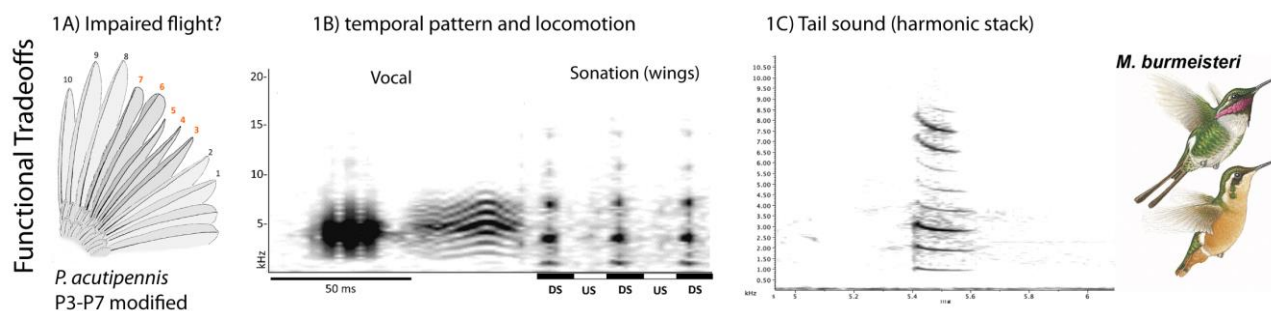


Figure 1. Tradeoffs with other functions. A) Sonations are often produced with modified wing morphology, as in adult male *Pseudocolopteryx acutipennis*. Images are from Jordan & Areta (4). B) Sonations are often produced during flight. C) A few birds produce sonations with the tail, such as adult male *Microstilbon burmeisteri*. Recording by R. Straneck, illustration from Pearman & Areta (40).

observed pattern is that species in which only the male produces sound, are also all dimorphic, which suggests that the morphology is selected against in females (13).

Some birds that produce sonations have modifications that are more than skin-deep: in manakins, Club-winged manakin and *Manacus* manakins each have modified wing bones (14, 15). Anecdotal observation has suggested that Club-winged manakin is a weaker flyer than other, less morphologically modified manakins (16), apparently on account of its modified wing bones. Experimentally testing this hypothesis (conducting simple flight tests on both sexes, plus a few outgroups) would be a way to formally test this hypothesis.

3.2 How do sonations coevolve with vocalizations?

The ‘transference’ hypothesis posits that redundancy between two signal types leads to a trade-off between the modalities; animals tend to have one or the other, but not both (17). For instance, male bowerbirds have transferred elaborate ornamentation from their own plumage, to the bower. There are a number of suggestions that sonations and vocalizations trade off. Ruffed Grouse defend their territory with a loud wing drumming (18), and are said to have a nearly non-existent syrinx. *Smithornis* broadbills likewise defend territories with wing sounds (3), and reportedly have few vocalizations and a puny syrinx (19). Essentially the same thing is reported for Club-winged Manakin (20). These instances are currently anecdotal: what is missing in each case is a formal phylogenetic analysis complete with examination of sonation-less outgroups, that tests whether the alleged shift in syrinx size actually coevolves on the same branch on which producing sonations evolved.

Another curious pattern that has been formally tested in one clade of hummingbirds is the apparent repeated evolution of ‘self-mimicry’. Specifically, some ‘bee’ hummingbirds (Tribe Mellisugini) sing, some produce wing trills (a repeated sound generated by wing feathers during flight), and most also produce sounds with their tail-feathers. Curiously, several of the singing species produce vocal songs that quite-closely resemble their own sonation (Figure 2A). Within a clade of about 37 species, this has evolved at least 4 times independently (6). Why this pattern has evolved remains unclear (6, 21). It is even possible for mechanical sounds to cross boundaries into different species. The “complex songs” of *Sicalis* yellow-finches contain imitations of vocalizations of other bird species (22). A recording of a male Greenish Yellow-finch (*Sicalis olivascens*) included a good rendering of the flight sound of a White-winged Ground-dove (*Metriopelia melanoptera*) (Figure 2C).

Are there other examples of coevolution of sonations and vocalizations? It seems there are, although critical details differ. In *Pseudocolaptes* flycatchers, all species produce a series of short introductory notes preceding a flourish. These introductory notes are vocal in all species, except for the Crested Doradito *P. sclateri* in which these consist of bill-snaps (23). Similarly, the flourish is exclusively vocal in three species, but consists exclusively of mechanical wing sounds in the Subtropical Doradito (4, 24) and of both mechanical and vocal sounds, in Dinelli’s Doradito *P. dinelliana* (24). These replacements of a vocalization with a

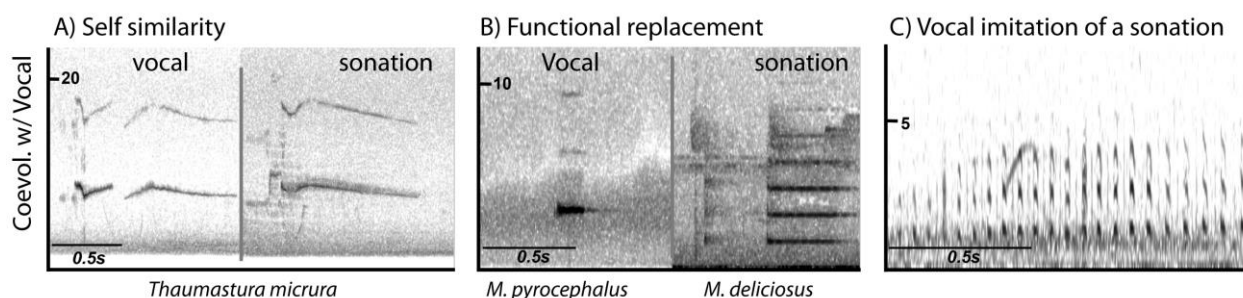


Figure 2. Sonations coevolve with vocalizations. A) Certain hummingbirds appear to have self “imitation”: they produce similar-sounding sounds both vocally and with their tail feathers. From Clark et al 2018. B) Several examples of functional replacement are known. Here, Fiery-capped Manakin (*Machaeropterus pyrocephalus*) defends its territories with vocal song, while congener Club-winged Manakin (*M. deliciosus*) defends its territories with a functionally equivalent sonation. Xeno Canto (XC777328 and XC750675). C) Sonations may even be imitated by species with vocal learning, such as this Greenish Yellow Finch (*Sicalis olivascens*) imitating Black-winged Ground Dove (*Metriopelia melanoptera*) wing sounds. Recording by A. Sureda.

Coevolution with behavior

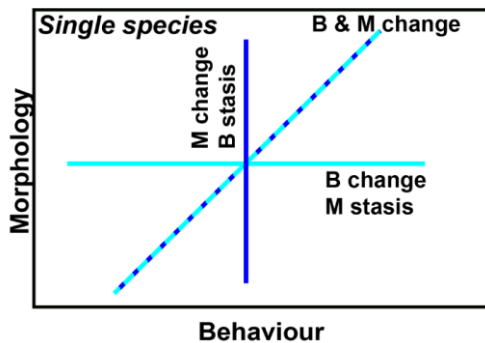


Figure 3. Morphology and Behavior together produce sonations. Either or both may evolve to change the acoustic form of sonations.

non-vocal element (or vice versa) might be linked to the ‘self-mimicry’ described, because, as an animal evolves from producing sound ‘A’ to sound ‘B’, one intermediate character state might be to produce both A and B. Another example of this seems to exist in *Machaeropterus* manakins. While Club-winged Manakin makes an amazing sonation with its wing feathers (25), its sister, *M. pyrocephalus* makes a similar-pitched flat vocalization (26) (Figure 2B). Examining the coevolution of sonations and vocalizations within manakins, in a phylogenetic context, would appear to be a fruitful endeavor.

3.3 How do sonations coevolve with behavior?

As argued above (§ 2), the initial condition for the evolution of sonations is the animal produces sound as a byproduct of something else, such as a visual display, or an incidental byproduct of locomotion. Clark and Prum (12) considered 69 independent origins of sonations and found that sonations most often evolve in the context of vigorous courtship display. One possible reason for this is rapid, vigorous motion is the most likely type of motions to generate sound as a byproduct (27). Another possible reason: sonations themselves might provide accurate information about the vigor of a display, since speed is correlated with pitch or sound pressure level (SPL), and in some contexts, ears may be better able to discriminate between subtle differences in performance, than are eyes. Thus, female receivers might find the sound of a courtship display to be informative about differences in male performance. While it is fun to speculate this hypothesis, testing it would be a substantial amount of work.

Quiet flight has evolved in owls and caprimulgids, in which several structural adaptations of the wings (e.g. leading-edge comb, dorsal velvet) seem to reduce the sounds of flight (28). And yet, paradoxically, some owls and some (possibly many) nightjars also make sonations by “wing-clapping” (29, 30). Thus, the same structural feature, the wings, are ‘designed’ to both produce less sound and more sound than normal. Whether and how these two opposite design attributes interact and what permits them to simultaneously coexist has not been investigated.

Another general question is: as an animal evolves sound-producing morphology and behavior, which evolves faster, behavior, morphology, or do the two coevolve at about the same rate (Figure 3)? In a study of ‘bee’ hummingbirds, Clark et al found that most species of hummingbird produce different sounds than their sister taxa, implying a high rate of morphological evolution in this clade. This study did not examine behavior *per se*, but based on the extremely high rate of morphological evolution, it would be difficult for behavior to evolve faster than morphology in this clade. By contrast, in woodpecker drumming, the morphology is constrained and only the behavior evolves (10). Cisticolas make snapping sounds but the sounds are very similar among species. Finally, manakins seem to be in between these extremes: *Manacus* manakins all sound the same, but other manakins (e.g. *Machaeropterus*) make different sonations. In total, the answer to this question might be it depends. And there is no generalizable pattern.

3.4 Do sonations occupy the same functional space as vocalizations?

The benefit of vocalizations is that the syrinx is capable of producing highly varied sounds. We do not know of any examples of sonations that take the place of nestling begging calls (although, nestling owls produce bill snaps in a variety of contexts), but otherwise, sonations appear to be functionally equivalent to most types of vocalizations (Figure 4). In pigeons wing sounds seem to replace alarm calls, signaling alarm when the animal takes off in a rush (since the wings are flapped faster than in a normal takeoff) (31, 32). In species such as broadbills or ruffed grouse, sonations advertise territory ownership (replacing undirected song), while in dozens of examples, sonations are used in directed communication with a potential mate. Bill-snaps figure prominently as agonistic sounds in tyrant flycatchers (33). In Subtropical Doraditos, sonations are incorporated into aerial displays and also during agonistic

male-male chases and are not known to play a role in mating (8). Because sonations tend to be more context specific than some vocalizations, the answer appears to be no, sonations do not (quite) occupy the same functional space as not-mechanical sounds (Figure 4).

Motivation-structural rules relating the quality of a sound to its context have been proposed for vocalizations (34). Whether similar rules follow for sonations has not been tested.

3.5 Do sonations occupy the same acoustic space as vocalizations?

Our impression is that the answer is no, but this is another question that is worthy of a formal phylogenetic test. Despite the virtuosity of the syrinx, and the fact that vocalizations seem to evolve quickly (frequently, sister taxa that are virtually identical in appearance sound different by voice), there is nonetheless a pervasive pattern: birds within focal clades tend to all be variations on a theme. That is, they have vocal resemblance. Parrots all squawk. Shorebirds have experienced “60 million years of vocal conservatism” (35). An experienced birdwatcher can go to a new continent, hear an unfamiliar song, and recognize it as belonging to *Turdus* (thrushes). Despite the finding that the syrinx permits a wide range of sound production and rapid vocal evolution, the evolution of vocalizations is nevertheless bounded.

Although most sonations are sexual signals, the best-studied exception are pigeons, where many of the sonations known within this clade are found in adults of both sexes (36), and the sonations serve as warning signals rather than sexual signals (31, 32). Another similar species might be Bourke’s

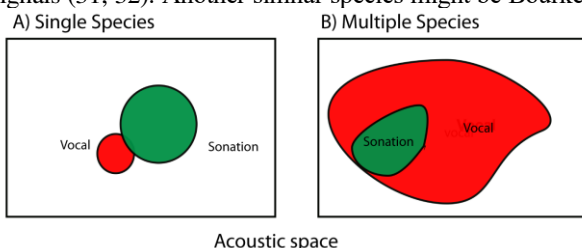


Figure 4. A) Within species, the acoustic space of sonations seems to be distinct from the acoustic space of vocalizations, although there may be overlap (Fig. 1A). B) Among species, vocalizations seem to be more versatile than sonations, and hence may occupy a larger space

parakeet (*Neopsephotus bourkii*), which also reportedly produces a trill in flight, but what function this trill has is unclear.

Because sonations are not subject to the same mechanical constraints as vocalizations, they permit a bird to make a totally different kind of sound. The example we are most familiar with is hummingbirds: hummingbird vocalizations and songs tend to all be high-frequency and squeaky (37). By contrast, their sonations can be low-frequency and melodious (to human ears), thus seeming to occupy distinctly different acoustic space than the respective vocalizations. Again, this observation bears formal testing, but we suggest that sonations permit an animal to expand the acoustic space available to it, and in some specific cases, sonations may occupy a larger portion of acoustic space than vocalizations (Figure 1). Of course, sonations are also bounded. For example, bill-snaps (produced by forcefully colliding the mandible and maxilla) are short, impulsive sounds across numerous clades. Wing sound features are often constrained by wing-flapping rates, and the physics of flutter (38, 39) and tail sounds seem to be largely constrained to be tonal because the tail itself is held static while another process (such as a high-speed dive) generates the conditions needed for sound. Ultimately, it appears to us that sonations occupy much, but not all of the acoustic space of vocalizations, because there seem to be few sonations that produce frequency-modulated tones, while frequency modulation is a prominent component of many vocalizations (Figure 1).

4. DISCUSSION

Here we have raised a series of testable hypotheses about the evolution of sonations. Some of these ideas have been tested in individual focal clades, such as hummingbirds or Doraditos, but these ideas bear testing in additional clades. The bird clades that have particularly high incidences of sonations are: Chickens (Galliformes), Nightjars (Caprimulgidae), Hummingbirds (Trochilidae), Doves (Columbidae), Shorebirds (Scolopacidae), Guans (Cracidae), Manakins (Pipridae), Cotingas (Cotingidae), new world Flycatchers (Tyrannidae), and Cisticolas (Cisticolidae). This list includes large families with species that do and do not produce sonations, and thus are suitable for phylogenetic analysis; small families that make sonations (Such as Lyre-tailed Honeyguide or *Smithornis* Broadbills) are less suitable for phylogenetic analysis because the production of sonations will have arisen on a long phylogenetic branch. It is our hope that we will spur

further research that formally tests some of the ideas expressed here. Many of the statements we have made are supported only for specific clades, or are based on anecdotal data. We eagerly await papers that robustly support (or refute) these ideas.

5. ACKNOWLEDGMENTS

CJC thanks the Fulbright Foundation for funding during preparation of this manuscript. A. Sureda shared her recording of *S. olivascens*.

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