

Chapter 4

Locomotion-Induced Sounds and Sonations: Mechanisms, Communication Function, and Relationship with Behavior

Christopher James Clark

Abstract Motion-induced sound is an intrinsic byproduct of essentially all animal behavior. Locomotion-induced sounds that have evolved specialization for communication are termed sonations. The null hypothesis is that locomotion-induced sounds are noncommunicative (adventitious), produced by nonspecialized morphology, and are involuntary. A sound is a sonation if it is produced by specialized morphology, or is produced voluntarily. The production of locomotion-induced sound can be examined at two levels: the animal motions (kinematics) that lead to sound production and the physical acoustic mechanism(s) that generate(s) the sound itself. The physical acoustics of locomotion induced sound are diverse, with both aerodynamic and structural mechanisms, including aeroelastic flutter, percussion, stridulation, and presumably many other undescribed mechanisms. There is a direct sound–motion correspondence between aspects of an animal’s motions and ensuing locomotion-induced sounds, especially in the time domain. This correspondence has two implications. One is experimental: sound recordings are a useful and perhaps underutilized source of data about animal locomotion. The second is behavioral: locomotion-induced sounds intrinsically contain information about an animal’s motions (such as wingbeat frequencies) that may be of interest to other animals. Therefore, locomotion-induced sounds are intrinsically suited to be mechanisms by which animals directly evaluate the locomotor performance of other animals, such as during courtship. The sound–motion correspondence is also a constraint. Sonations seem less acoustically diverse than vocalizations. Because they require discrete behaviors to be produced, animals also have somewhat fewer opportunities to produce sonations strategically, and few sonations are frequency-modulated. Sound production mechanisms of sonations are external to the animal and therefore are easy to manipulate experimentally on wild animals, making sonations an ideal, underutilized system for testing hypotheses about acoustic function.

C.J. Clark (✉)
Department of Biology, University of California, Riverside,
Riverside, CA 92521, USA
e-mail: cclark@ucr.edu

Keywords Adventitious • Communication • Flight • Flutter • Hummingbird • Kinematics • Manakin • Mechanical sound • Nonvocal • Voluntariness • Wing

4.1 Introduction

Many vertebrates produce nonvocal communication sounds, which are sometimes called mechanical sounds (Manson-Bahr and Pye 1985), particularly with respect to birds. Humans are no exception: we applaud a performance by clapping our hands or announce our presence by knocking on a door. Many of the best-known nonvocal signals are produced by birds, including the winnowing displays of snipe (*Gallinago* and *Coenocorypha* spp.), wing snaps of manakins (Pipridae; Fig. 4.1), or the diverse wing and tail sounds produced by displaying hummingbirds (Darwin 1871).

Examples apart from birds include ground thumping in rodents and other mammals (Randall 2001), tail rattling of rattlesnakes, or stridulation of modified spines in streaked tenrecs (*Hemicentetes semispinosus*) (Endo et al. 2010). Nonvocal acoustic communication has evolved hundreds of times, and as essentially any body

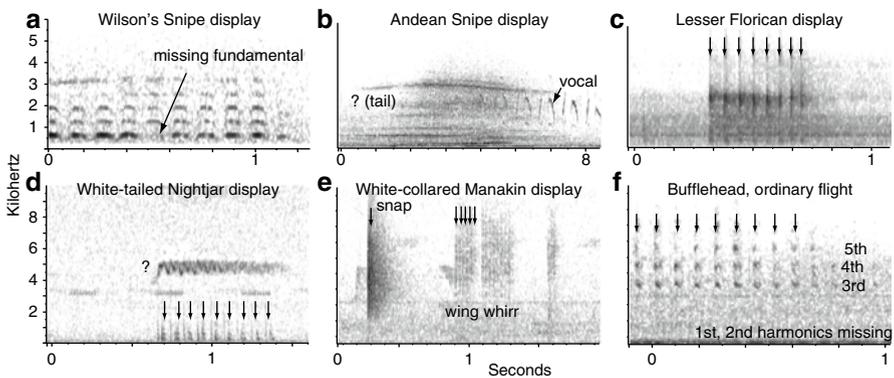


Fig. 4.1 Examples of the diversity of locomotion-induced sounds of birds. Vertical arrows indicate sound produced during wingbeats; question marks indicate physical mechanism is unresolved. (a) Male Wilson's snipe (*Gallinago delicata*) produces pulses of tonal sounds with its outer tail feathers during a dive display; arrow indicates a missing fundamental (source: XC #13808). (b) Male Andean snipe (*G. jamesoni*) produces multiple frequencies of sound, presumably with the tail, during a dive (XC #2014). (c) Male lesser florican (*Sypheotides indicus*) produces a knocking sound with the wings during a jump display (sound from Bhatt and Bardolia 2006). (d) Male white-tailed nightjar (*Hydropsalis cayennensis*) produces a tonal sound via an unknown mechanism during a flight display (ML #60664). (e) Male white-collared manakin (*Manacus candei*) produces two different types of sonations in display, first a snap and then a wing whirr (the latter was termed "snort" by Bostwick and Prum 2003; ML #72655). (f) Bufflehead (*Bucephala albeola*) of unknown sex produces tonal sound produced during ordinary flight. The third to fifth harmonics are present while the first and second harmonics of sound are missing (ML #57549). Note differing timescales of spectrograms; FFT: 512-sample Hann window, 50 % overlap. Sound source abbreviations: XC, www.Xeno-Canto.org; ML, Macaulay Library, macaulaylibrary.org

part can produce sound, nonvocal sounds are more diverse morphologically (though probably not acoustically) than vocal communication mechanisms. This chapter explores general features in connection with how these sounds are produced by terrestrial vertebrates, a brief overview of some of the physical acoustic mechanisms, their relationship with behavior, and what is known about how they evolve.

The evolutionary origin of communicative sounds is clear: They arose out of incidental byproducts of behaviors (adventitious sounds) that were converted to communication sounds after receivers attended to them (Darwin 1871; Ewing 1989). This occurs because virtually all motions generate sound, including inanimate motion, such as splashing of water or whooshing of wind in the trees. Sounds and vibrations are also an omnipresent byproduct of all animal motions, including the familiar rustling of a mouse or lizard scurrying through dry leaves, or the whoosh of the wings of a bat or bird that passes close by. Perhaps motion-induced sounds are underappreciated because they often do not have a particular communication function and can be unwanted noise that obscures a vocalization of interest. Everyday experience suggests that it is moving relatively silently that is difficult, such as a stalking cat or hunting owl, or as anyone trying to slip unnoticed out of a quiet room can attest.

These observations provide an axiom with two parts. First, all animal motions (i.e., nearly all animal behaviors) produce sound, audible or not. Second, the converse is also true: All significant animal sounds arise from a behavior. Therefore, study of animal bioacoustics can encompass nearly all of animal behavior. These two fields, animal behavior and bioacoustics, are partially divorced in practice because vocalizations of terrestrial vertebrates arise mostly from behaviors of the larynx or syrinx, structures specialized for the production of sound, whereas most other behaviors and morphology are irrelevant to vocalizations. These neat distinctions become blurred when nonvocal sounds are considered. Although all behaviors make sound, the issue is whether these sounds are audible. Further, every part of an animal is a sound-producing structure, even if not specialized for sound production. These features produce conceptual challenges: Simplifying assumptions that are usually reasonable for vocalizations, such as that they are voluntary, or function for communication, are often not reasonable for nonvocal sounds. This chapter explores these issues in more detail. Birds have been a focus of some recent work, and this chapter focuses preponderantly on them (Fig. 4.1).

4.1.1 Definitions

It is difficult to define a term by what it is not, so this chapter defines nonvocal sounds as locomotion-induced sounds. Broadly, all behaviors can be classified as locomotion, eating, or breathing (Barlow 1967). Of these three, nonvocal sounds physically originate from locomotion and are largely produced by interactions between the animal's integument and the environment. Eating and breathing, by contrast, are coupled pharyngeal functions and the associated morphology forms

the vocal tract. Vocalizations, broadly defined, are the acoustic byproducts of the behaviors of eating or breathing. Vocalizations originate from motion inside the animal and include sounds made by fluid as it leaves the animal. Included under this broad definition of vocalization are the “voiced” sounds of the larynx or syrinx, and also “voiceless” sounds such as human whispering, sneezes, coughing, tongue clicks, bill snaps, chewing, and even passing gas. A narrower definition would consider vocalizations to include only “voiced” sounds of two nonhomologous structures, the larynx and syrinx (e.g., Au and Suthers 2014). This strict-sense definition of vocalizations would treat as nonvocal bill snaps and communication farts (Wilson et al. 2003), but by this count, also nonvocal are dolphin calls and human whispers (Au and Suthers 2014)! Such a broad definition of “nonvocal” is not useful, as whispering and communication farts have more in common with the “voiced” sounds generated by the larynx/syrinx than with locomotion-induced sounds. Therefore, this chapter employs the broad definition of vocalization, and nonvocal sounds are only those produced by behaviors related to locomotion.

Nonvocal sounds can be categorized either descriptively or functionally, and neither naming scheme is perfect. Considering function, adventitious sounds are incidental byproducts of motion that lack communication function. Darwin (1871) was the first to propose that these incidental sounds may be co-opted for communication, which he termed instrumental music. This poetic term did not enter popular usage, and the nonvocal sounds of birds instead came to be called mechanical sounds, without reference to function (Manson-Bahr and Pye 1985). Bostwick and Prum (2003) proposed the term “sonation” to mean nonvocal sounds modulated *and evolved* for communication function, where “sonate” is the corresponding verb. This term was to be analogous to the word phonation, which describes strict-sense vocalizations. One major problem arises from attempts to use the term sonation rigorously, however. Most syrinx/larynx sounds are likely to be functional and not adventitious, and so it is reasonable to assume they are phonations, even if the function is totally unknown. By contrast, it is often not clear whether a particular nonvocal sound has evolved for communication, and is therefore a sonation. Assuming that an unstudied phonation has a function will only rarely be controversial. By contrast, most nonvocal sounds are not communicative, and diagnosis of a sonation can be tricky and assumption laden. Therefore, the label sonation cannot be applied indiscriminately.

There are two principal criteria used to diagnose a sonation: specialized morphology and voluntariness. The easier criterion to apply is specialized morphology. If the morphology used to make the sound has evolved a functional form closely linked to the acoustic form of the sound, it is almost certainly a sonation. For instance, rattlesnakes have evolved a rattle, tenrecs have evolved modified spines, or many birds have evolved feathers with highly specialized shapes, and none of these morphologies have functions besides production of sound. These are reasonably assumed to be sonations, even if the sound is not voluntary, per the second criterion.

Morphology is often not obviously specialized for sound production. The second best criterion for a sonation is voluntariness, whether the sound is produced

intentionally and production can be modulated by the animal. This complex topic is discussed further at the end of Sect. 4.2.1. Voluntariness is clearest when the kinematics (behaviors) that produce the sound are distinctive and specialized for sound production.

Even with these two criteria, ambiguous cases are not hard to find, even in human behavior, where intent can be deciphered. Human footsteps are normally adventitious and yet contain information used by others. One might recognize the approach of a particular colleague by his or her footsteps. Yet footsteps are also sometimes voluntarily modulated; for instance, that colleague might tiptoe to avoid alerting someone to his or her presence. Is tiptoeing communication? It fails the morphology criteria (feet/shoes do not seem adapted for acoustic communication) and the sounds produced are not voluntary either. The related behavior of tap dancing is a sonation, the product of cultural evolution. Thus, tap dancing is arguably a sonation, whereas distinctive, individual-specific footsteps are not.

Consider another example: If a person puts a bell on a cat or a horse that then jingles when the animal walks, is the resulting sound a sonation, or adventitious? It is modified morphology; it is not voluntarily modulated by the animal as it walks, but it is voluntary in the sense that the bell was placed voluntarily on the animal. It also *is* an attempt to communicate, by the human. However, if the purpose is to alert birds to the presence of the cat, it is arguably not a sonation, because birds have not evolved, or learned, to be aware that jingling is a signal of approaching danger. On the other hand, if the bell is to alert other people of an approaching horse, it is a sonation.

In neither of these examples is this logic iron clad: Both human footsteps and bells on animals are debatable sonations. The important role of learning has been ignored, and as the context is human behavior, intent is easier to assess than it is in animal behavior. It is often not clear *a priori* whether many types of nonvocal animal sounds are sonations or adventitious; function is a hypothesis to be tested, not assumed. The conservative approach is therefore to use the term sonation only when there is distinctive morphology or behavior obviously associated with the production of the nonvocal sound, or after experiments testing function. This means that many locomotion-induced sounds that might be sonations cannot be immediately recognized as such.

As an alternative, sounds can be named in the context of the underlying behavior, neutral to possible function. For instance, sounds produced in flight are “flight sounds,” those produced during displays are “display sounds,” and so forth. Some such sounds already have their own vernacular names, such as footsteps or clapping. In addition to functional neutrality, such a name should be descriptive and not imply a particular physical acoustic mechanism if the aptness of that mechanism is unclear. For instance, snapping, clapping, and drumming are related percussive mechanisms with distinctive acoustic forms and are often appropriate names, as in “wing clapping.” But other widely used terms are misnomers. For instance, many sounds produced by bird wings have been called “wing whistles” as a description of their tonality (Miller and Inouye 1983; Barrera et al. 2011). However, a whistle is a specific aerodynamic mechanism that produces highly tonal sound that is often high

pitched (Wilson et al. 1971). This aerodynamic mechanism, although common in wind musical instruments and certain mouth-generated human vocalizations (Fletcher 1992; Fletcher and Rossing 1998), has not been demonstrated for any nonvocal sound. The bird sounds called “wing whistles” are instead produced by aeroelastic flutter (Clark et al. 2013b). Whistle is also not a suitable synonym for tonal, because mechanisms involving mechanical (structural) resonance also produce tonal sound, such as the sound of a plucked guitar string, and one would not say “the plucked guitar string whistled pleasantly.”

The disadvantage of a descriptive naming scheme is it can be cumbersome without pointing to whether or how the sound is biologically interesting.

4.2 Mechanisms

The physical mechanisms that produce locomotion-induced sounds derive from an interaction between morphology and behavior. The analogy of a musical instrument is apt: an animal’s morphology is the instrument while its behavior is how the instrument is played. Section 4.2.1 explores the relationship between kinematics (motions) and sound, with emphasis on an experimental perspective. This topic, kinematics, is revisited in Sect. 4.3.1 from a functional perspective and the role of kinematics in communication. Later parts of this section provide a qualitative overview of the physical acoustics of locomotor-induced sound. This topic, and especially Sect. 4.2.5 (solid interactions), has been too poorly studied to allow a comprehensive overview. Entirely neglected are physical acoustics of locomotion-induced sounds that originate inside the animal, such as rattlesnake tail-shaking, clicking of tendons/ligaments across bony processes in joints, as in reindeer (*Rangifer tarandus*) and other ungulates (Bro-Jørgensen and Dabelsteen 2008), or “cracking” of joints, as in human knuckles, which is caused by cavitation of dissolved gasses in synovial fluid (Unsworth et al. 1971). Moreover, as Parmentier and Fine (Chap. 2) and Narins et al. (Chap. 7) address hydroacoustics and seismic communication respectively, only examples from airborne nonvocal sound are provided.

4.2.1 Animal Kinematics and Sound

Locomotion is a key component of animal natural history. Every motion an animal performs has an acoustic signature. This acoustic signature contains information about the animal’s motions, potentially revealing its location in space, its velocity, and especially, discrete events of locomotion such as individual footfalls or wing flaps. The information contained in these sounds might be used by a potential receiver (Sect. 4.3), or experimentally useful to a scientist. In the context of describing the courtship dive of Anna’s hummingbird (*Calypte anna*), Clark (2009) termed the relationship between sound and motion a “1:1 correspondence” because the

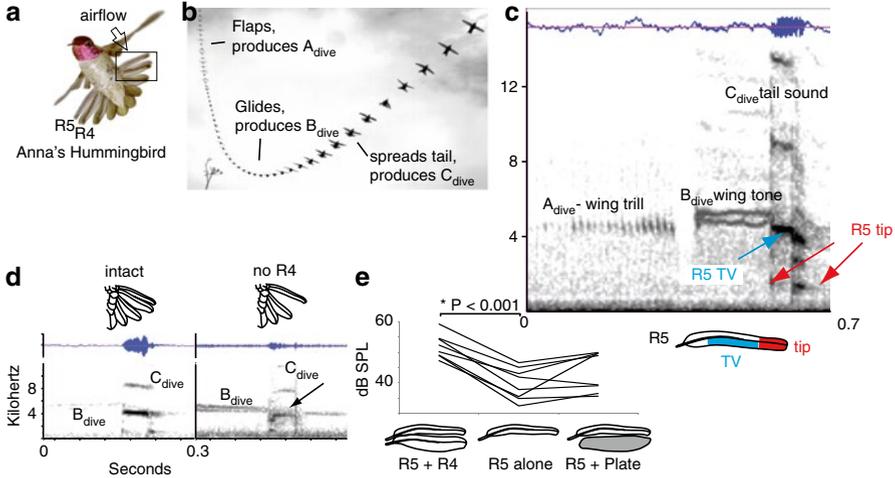


Fig. 4.2 Male Anna’s hummingbird dive and produce sound with the wings and two tail-feathers, R5 and R4. (a) Male Anna’s hummingbird (*Calypte anna*), with approximate direction of airflow over the tail during a dive. (b) Wing and tail kinematics during the dive correspond to sounds A_{dive} , B_{dive} , and C_{dive} produced during the dive. (c) Dive sound. Within C_{dive} , two sounds are produced: an approximately 4-kHz sound produced by the trailing vane (TV) of the feather R5 (teal), and a second, an approximately 1.2 kHz sound is produced by the tip of R5 (red) as the tail is spread and shut (*note*: the tip mode is particularly pronounced in this recording). (d, e) Feather R4 amplifies the dive sound through aerodynamic sympathetic vibration. (d) Removing R4 from a bird reduces amplitude of the dive sound. (e) Tested in a wind tunnel, presence of R4 increases SPL by 12 dB, because R4 vibrates in response to R5’s flutter, whereas a flat plate as a control does not [a, d, e modified from Clark, Elias, & Prum (2011)]. Aeroelastic flutter produces hummingbird feather songs. *Science*, 333, 1430–1433. Reprinted with permission from AAAS. b modified from Clark (2009) under the author’s copyright]

observed kinematics have a component frequency or timing that, after accounting for measurement error, exactly matches the frequencies or timings in the associated sound (Fig. 4.2b, c).

This correspondence does not imply that all animal motions are audible. Rather, given detection of locomotion-induced sound, temporal patterns within the sound must exactly match some aspect of the underlying motions of the animal, after correcting for the sound delay and other sources of error. The sound delay is the result of the difference between speed of light, which is nearly infinite, and the speed of sound in air (c), which is approximately 340 m s^{-1} , and varies slightly with temperature. For synchronized video and sound recordings, where the video is recording at a frame rate of $n \text{ frames s}^{-1}$ and the microphone is distance (d) meters from the animal, the lag (l) in video frames is

$$l = nd / c \tag{4.1}$$

The effect of sound delay is thus exacerbated when recording with high-speed video (high n) or at significant distances (d) from the subject.

The direct correspondence between sound and motion has broad utility in experimental design. A sound recording of a behavior can yield much of the same information as a video. For instance, a sound recording reveals stride frequency of a walking animal, or wingbeat frequency of a flying one (Ortiz-Crespo 1980; Hunter and Picman 2005). Some behaviors are easier to record with sound than with video, owing to the ability of sound to go around minor obstacles, lack of a need to focus, and the wider field of reception of microphones.

That said, the relationship between sound and motion is sometimes subtle, and connecting sounds with motions requires assumptions or prior knowledge about how the sound is produced. For example, in a flight display called the pendulum display (Fig. 4.3), a male Allen’s hummingbird (*Selasphorus sasin*) rapidly flips his tail up and down in time with pulses of a “chirruping” sound (Aldrich 1939; Mitchell 2000). This exact match between tail motions and sound suggested to observers that these chirruping sounds were produced by the tail (Aldrich 1939; Mitchell 2000); the wings were flapped too fast to see with the naked eye. However, experimental evidence overturned this initial assessment. Birds missing their tail still produced these chirruping sounds (Clark 2014), and a high-speed video of the display revealed that when producing the chirruping sounds, the birds, in addition to moving their tail, also changed their wing kinematics, briefly flapping the wings with a contralateral asymmetry, so that a 1:1 match also existed between these asymmetrical wing motions and sound. The dorsoventral tail motions, though obvious to the naked eye,

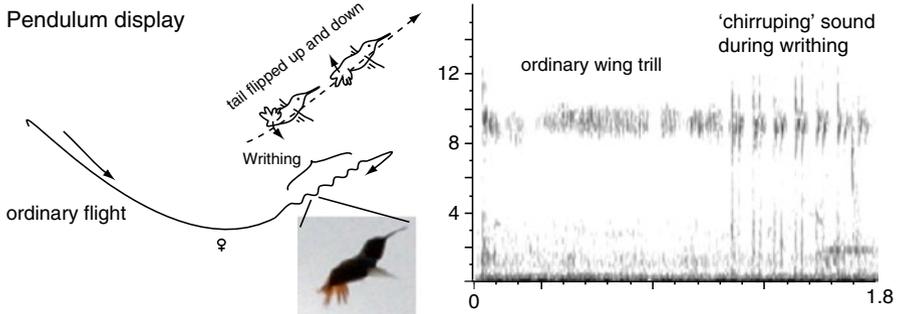


Fig. 4.3 Male Allen’s hummingbird (*Selasphorus sasin*) pendulum display shows why the principle that sound and motion correspond directly must be applied carefully: Not all correlations are causal. Male Allen’s hummingbirds produce an ordinary wing trill during all modes of flight. In the pendulum display, males fly in a shallow U over a female (left). On the downswing of the display, ordinary flight produces the ordinary wing trill, while on the upswing, the male “writhes.” This writhing is apparent to the naked eye as a rapid flipping up and down of the widely spread tail (left); the wings, by contrast, are a blur. Produced in exact synchrony with writhing are pulses of “chirruping” sound (right). The exact synchrony of the tail-flipping with the pulses of “chirruping” led previous workers to suggest the tail produces the chirruping sound (Aldrich 1939; Mitchell 2000). However, this is incorrect: The chirruping sound is a modified version of the wing trill, produced by changes in wing kinematics that are visible only with a high-speed video. The tail’s motions are correlated with sound production because the tail produces balancing forces against the atypical wing kinematics, not because the tail itself produces sound (Clark and Mitchell 2013)

were simply correlated with the asymmetrical wing motions, which actually produce the sound (Clark and Mitchell 2013).

This example demonstrates that inferring sound production from casual observation of kinematics alone may be misleading, and manipulative experiments (Sect. 4.2.2) that test the physical mechanism provide a stronger inference as to how the sound is produced.

4.2.1.1 Voluntariness

An important kinematic issue is sometimes not trivial to discern: To what degree is a locomotion-induced sound produced voluntarily? Voluntariness is the degree to which the animal can modulate the sound *independently* of the kinematics of ordinary motions, thereby permitting it to produce the sound strategically. For instance, many hummingbirds produce specialized wing sounds (wing trills) during ordinary flight, which seem muted or even silent during hovering, but are loud during sharp maneuvers and high-speed flight (Clark, pers. obs.). To what degree are these acoustic differences voluntary, allowing the animals to become stealthy or noisy if they wish?

The voluntariness of locomotion-induced sounds falls along a spectrum. Although the two ends of this spectrum, completely voluntary and entirely involuntary, are reasonably clear, intermediate examples are harder to diagnose and may require experimentation. Sounds easily identified as voluntary have two properties: (1) the sound requires specific, easily identifiable gross kinematics to produce and (2) these kinematics seem specialized for sound production. For instance, a hummingbird spreads its tail to make sound at only a specific point of its dive display, or a manakin snaps its wings together with kinematics not observed in ordinary flight (Bostwick and Prum 2003; Clark and Feo 2008). In these cases it is reasonable to assume the sound is voluntary, without detailed experimentation. Involuntary sounds instead have the following two properties: (1) the gross kinematics that produce them are general, not specific, and (2) the sound is always produced during general locomotor behavior. For instance, turbulence-induced whooshing sounds, although faint, are always present during bird flight. The only way an animal can modulate involuntary sounds is by changing the underlying behavior, such as by ceasing locomotion altogether.

In between these two extremes are cases where the voluntariness of the sound may be hard to assess. These are locomotion-induced sounds that do not have a distinct, obvious kinematic correlate, but they are also intermittent, observed in some types of seemingly ordinary locomotion, but not others. The tonal wing trills of many doves are an example; casual observation indicates these sounds are produced by only some individuals and/or in only some flight contexts (particularly during takeoff). Barrera et al. (2011), in a study of alarm function of the wing trill of zenaida dove (*Zenaida aurita*), implicitly assume the wing trill is voluntary because it is not produced in all modes of flight. However, production of a sound in only some contexts does not mean the sound is under voluntary control. Instead, the kinematic conditions necessary for involuntary production may be specific. Flutter

of a wing feather (the likely physical mechanism underlying most tonal wing trills in birds, such as doves) requires local air velocity to exceed a threshold, U^* . The simplest explanation of a sound observed in some motions and not others is that U^* is exceeded in some cases but not others. Thus, a pigeon taking off normally (unalarmed) may be relatively quiet because it does not flap its wings quite fast enough to exceed U^* and produce sound, whereas a pigeon taking off in alarm, with only a small change in kinematics, does exceed U^* and produce tonal sound. This need not be voluntary.

Designing experiments to test whether a sound is voluntary requires an appropriate null model. As involuntary sounds abound in nature and this is clearly the ancestral character state if one goes far enough back in the phylogenetic tree, involuntary control is the null. Voluntary control of sound is often the derived character state, and is best regarded as the alternate hypothesis. Under this null, sound production is physically, strictly constrained and prescribed by gross locomotor kinematics. For sounds produced in apparently normal kinematics, the alternate hypothesis holds that the animal must alter something, an “invisible switch” (i.e., not easily observed within seemingly ordinary motions), to turn sound on or off, without otherwise affecting locomotion. For instance, perhaps pigeons produce the wing trill voluntarily because they are able to alter a subtle component of their wing kinematics to turn wing trill production on or off, with little overall effect on flight. There are many ways this could occur. For instance, suppose they slightly change wing pronation at the beginning of the downstroke, and this affects bending or overlap of a crucial feather relative to its neighbor (nonoverlap is essential for flutter: Feo and Clark 2010), thereby activating sound production without otherwise affecting locomotion. Such a kinematic change is “invisible” because it would be hard to detect.

Unfortunately, obtaining the right data to clearly reject this null will sometimes be difficult, even when the null is in fact incorrect. The most intuitive approach is to record the animal’s motions when producing and not producing the sound of interest, and search for a general kinematic correlate with sound production. However, this approach may be frustrating and inconclusive, for the switch itself may not be easily revealed. The simplest prediction the invisible switch hypothesis makes is that sound production does *not* correlate with gross kinematics, which is problematic because the absence of a correlation always has alternative explanations. By contrast, it will be easy to fail to reject the null; the null predicts some general kinematic variable will be different in sound-producing versus non-sound-producing kinematic contexts. For instance, the null predicts alarmed pigeons flap their wings faster on average than nonalarmed (notwithstanding spurious correlations; Sect. 4.2.1). Instead, to support the invisible switch hypothesis, an experimenter must find the switch itself, which constitutes the exact physical features that produce sound, and what kinematics the animal uses to turn sound production on and off. The experimenter must show (or argue) that changing these kinematics is not otherwise a crucial component for locomotion, and is therefore under voluntary control.

4.2.2 *Experimental Approaches*

Nonvocal sounds are, by definition, produced by an animal's external morphology. This affords easy access to the hypothesized sound source, facilitating experiments on the physical mechanisms of sound production with relatively benign effects on the animal, as has been done on hummingbirds (Miller and Inouye 1983; Clark and Feo 2008) and snipe (Tuck 1972). Whereas most manipulative experiments have sought to identify the physical origin of sound, Miller and Inouye (1983) tested function by using glue to silence the wing trill produced by the tips of the outer wing feathers of territorial male broad-tailed hummingbirds (*Selasphorus platycercus*). They found that these silenced males then tended to lose their territories, but regained them once the glue was removed; control birds with glue on non-sound-producing wing feathers were not as strongly affected. Miller and Inouye's (1983) study demonstrates the feasibility of performing field manipulations to study the ecological context and function of locomotion-induced sounds using simple experiments. Birds in particular are highly amenable: Feathers, if experimentally plucked, are regrown in a few weeks.

Feathers used for sonations often have a noteworthy shape, but not all unusually shaped feathers produce sound—and what constitutes an “unusual” feather shape may not be clear *a priori*. The most rigorous way to show that a given structure produces a particular sound is to demonstrate that the structure is both necessary and sufficient to produce the sound. Tests of both necessity and sufficiency can be feasible on feathers and are therefore an appropriate starting point for studies of function or evolution. More limited data, such as on sufficiency alone, can be ambiguous. For instance, essentially all feathers tested in a wind tunnel can flutter and are sufficient to generate sound, as discussed further in Sect. 4.2.4, and so this type of data by itself does not provide strong grounds for concluding that a feather actually does produce sound in flight (Clark et al. 2013a, b).

Paired experiments that demonstrated both necessity and sufficiency settled disagreement on the nonvocal origin of sonations in hummingbirds (Bostwick 2006). Male Anna's hummingbirds produce a loud *chirp* (the dive sound) during a display dive (Fig. 4.2). Rodgers (1940) demonstrated sufficiency by finding that whipping the outer tail feather through the air produced a sound similar to the *chirp* (see also Aldrich 1939). But Baptista and Matsui (1979) argued the dive sounds were vocal, owing to spectral similarity between the dive chirp and a portion of the species' obviously vocal song. Moreover in the sister species, Costa's hummingbird (*Calypte costae*), the dive sound and entire song were nearly identical to each other (Baptista and Matsui 1979; Baptista 2001). Neither side had tested whether tail feathers are necessary for the dive sound, so Clark and Feo (2008) resolved the disagreement by showing that removing the outer tail feathers from territorial males completely eliminated the bird's ability to produce the chirp. They also replicated Rodger's (1940) result, demonstrating the same feathers were sufficient to produce the sound. As the vocal versus nonvocal origin of other hummingbird sounds had been questioned (Baptista and Matsui 1979; Pytte and Ficken 1994), Clark and Feo performed

similar experiments on Costa's (Clark and Feo 2010), black-chinned (*Archilochus alexandri*: Feo and Clark 2010), Calliope (*Selasphorus calliope*: Clark 2011), and Allen's hummingbird (*S. sasin*: Clark 2014). They showed that in every case, sounds of disputed origin were nonvocal.

To date, there seem to be no cases in which a bird sound claimed to be nonvocal was later demonstrated to be vocal. Every debated instance has turned out to be nonvocal, implying that if it does not sound vocal, it probably is not. On the other hand, there are many instances in which the hypothesized mechanism was incorrect (Clark 2008; Fig. 4.3). Therefore, a logical starting point for experiments on apparently nonvocal sounds is with simple tests intended to verify the mechanistic origin of sound. For instance, the streaked tenrec produces sound with modified hair (Endo et al. 2010), and videos seem to imply the mechanism is frictional (BBC 2011). A possible starting point for a study of function would be to test what happens to sound production when one or more of the modified hairs is removed or otherwise manipulated.

4.2.3 *Physical Mechanisms*

There are multiple physical mechanisms by which motion generates sound, in two categories: aerodynamic mechanisms and solid mechanisms. This is perhaps an oversimplification, and this section does not provide an extensive overview of physical acoustics. Major issues, such as of impedance and other mechanisms that modulate amplitude, are ignored. Instead this section provides a brief overview of the physical acoustic mechanisms known or hypothesized to contribute to locomotion-induced sounds.

Physically speaking, sound is vibration of fluid, a longitudinal oscillation in which both fluid pressure and velocity vary at a point in space (Ewing 1989; Fletcher 1992). The magnitude of the velocity component is high in the near field, close to the source, but diminishes and is nearly negligible in the far field, away from the source. Because sound is oscillating (changing) pressure and velocity, it therefore originates from any process that results in a *change* in local fluid pressure or velocity. All accelerations and structural vibrations therefore produce sound.

4.2.4 *Aerodynamic Mechanisms*

Aerodynamic origins of sound involve air flowing around a solid object. Sound is generated by any flow conditions that produce a change in pressure at a point on the surface of the object. Change in pressure of a point arises as a necessary consequence of unsteady or dynamic motions, meaning the motion has a significant (non-zero) acceleration. All animal motions have a dynamic component, and any temporal part of an animal accelerates, it displaces the surrounding fluid (air or water),

resulting in a change in pressure. Some of this pressure change radiates away from the animal as longitudinal pressure waves. As most animal motions are low frequency, the resulting sound is infrasound, and will often be inaudible. This simple mechanism explains the humming sound of insect wings (Sueur et al. 2005; Bae and Moon 2008) and hummingbirds; these are audible because the wingbeat frequency itself is audible. As it is a physical consequence of production of aerodynamic force, Lentink et al. (2015) have shown that infrasound produced by a flying animal may be used to measure the underlying aerodynamic forces that were generated in flight. So although these sounds are largely biologically inconsequential, measurement of flight infrasound may be a technique with further applications for study of the biomechanics of flight.

More complex aerodynamic interactions arise from generation of turbulence, an aerodynamic mechanism that applies to all flying vertebrates (Vogel 1994). Turbulence, which is random fluid motion, can be modeled as a random or semirandom spectrum (in both space and time) of vortices with varying angular velocities (frequencies) and strengths, where a single vortex is a spinning packet of fluid (Blake 1986; Vogel 1994). Turbulently moving fluid is more or less the aerodynamic near field; turbulence flowing past an ear generates low-frequency, atonal sound as a near-field effect, such as the whooshing sound of waving a hand close by one's ear. Turbulence generated by air flowing past a microphone produces the same effect and is the reason microphones often require windscreens.

Vortices have low-pressure centers, meaning that each time a vortex changes strength (forming or dissipating), there is a change in this pressure, resulting in sound (Blake 1986). A vortex dissipating away from a solid structure, such as in an animal's wake, apparently produces relatively little sound, because an isolated vortex acts as a quadrupole sound source,¹ an inefficient radiator of sound (Blake 1986). By contrast, a vortex that forms adjacent to a solid such as an animal's wing or body will act as a dipole sound source, a more efficient radiator of sound. As vortex formation is often random with most energy at low frequency, the sound of turbulence forming is atonal and low frequency (Blake 1986). These vortex formation/dissipation mechanisms are the likely origin of the whooshing sounds animals make in flight, such as the flapping sounds passerine birds produce in ordinary flight (Fournier et al. 2013).

Owls that hunt by ear have multiple wing features that change how turbulence develops on the wing, shifting the vorticity power spectrum toward lower frequencies (Kroeger et al. 1972; Sarradj et al. 2011; Geyer et al. 2013). The amplitude of vortex-induced sound rises with a high power of velocity (Lighthill 1952), so owls also reduce their acoustic signature by flying slowly, and only in fast-flying birds, such as the stoop of a peregrine falcon (*Falco peregrinus*) or aerial dive of a marbled murrelet (*Brachyramphus marmoratus*, which produces a loud jet-like sound:

¹Dipoles and quadrupoles are models of sound sources, where a dipole is two adjacent sources of opposite phase, and a quadrupole is four adjacent sources of alternating phase; see p. 171 of Fletcher and Rossing (1998).

Nelson and Hamer 1995) are turbulence-generated whooshes audible at distances of tens of meters.

Another aerodynamic mechanism is whistling, a term sometimes mistakenly applied to locomotion-induced sound on account of the sound's tonality. There are multiple types of whistles, the simplest of which produce tonal sound through vortex formation that is not random, but is driven at a particular frequency by an *aerodynamic* feedback mechanism. Such a mechanism is the result of an aerodynamic interaction with a solid structure. The sound of the wind whistling in one's ear or at the corner of a building are examples (Blake 1986; Fletcher 1992). Whistles are often coupled to (and the acoustic frequency driven by) air-filled cavities that act as Helmholtz resonators² (Fletcher 1992) such as the human mouth during whistling (Fletcher and Rossing 1998). Mechanical resonance (dynamic feedback from the solid structure) is unimportant to whistles. Although most human-designed whistles are associated with rigid structures, the structure could vibrate. If it does, under the whistle model it vibrates in forced response to fluid flow, as a vortex-induced vibration. No examples of whistled nonvocal sounds are yet known in animals. Sounds produced by flying birds are sometimes called "wing whistles," but this name appears to be a functional misnomer and no bird is known to actually whistle with its wings or tail (Clark et al. 2013b). Instead, the available evidence implicates wing stiffness and structural resonance as having an important physical role in these sounds, meaning they are instead produced by a different mechanism, aeroelastic flutter.

Aeroelastic flutter, or flutter for short, is a dynamic interaction that is the result of coupling between aerodynamic forces and the structural properties of a stiff, flat object such as a feather in flowing fluid. Flutter is the mechanism by which hummingbird feathers produce sound (Clark et al. 2011). Above a critical velocity, U^* , energy from the airflow overcomes damping and the feather spontaneously oscillates at a structural resonance frequency (Clark et al. 2013a, b). Nearly all flutter described thus far has been limit-cycle (periodic) flutter, in which the feather flutters at a discrete frequency, plus harmonics. Chaotic (non-limit cycle) flutter is possible (Alben and Shelley 2008), and occasionally individual feathers tested in a wind tunnel flutter this way, although no cases of chaotic flutter in actual bird flight are yet documented (Clark et al. 2013a). The frequency and mode shape³ of flutter are set by local flow conditions (feather orientation relative to flow, air speed, presence of neighboring feathers) and also feather resonance properties (stiffness, size, shape). Changes in any of these independent variables can produce both linear and nonlinear responses in flutter frequency. The resulting sound is tonal with strong (sometimes dominant) harmonics, with frequencies ranging from a few hundred

²A Helmholtz resonator is a cavity with a characteristic aerodynamic resonance determined by its geometry. For example, blowing across the top of an empty beer bottle causes it to act as a Helmholtz resonator.

³Mode shape is the "shape" of a resonance frequency (normal mode) of a structure, that is, the distribution of motion of all points across a structure at a given frequency, when that structure is mechanically excited in an ideal way. Airflow is not an ideal source of excitation, so technically speaking, a fluttering feather exhibits not a mode shape but an *operating deflection shape* (Richardson 1997). This subtle distinction is ignored here, following Clark et al. (2013a).

hertz to as high as 10 kHz (Clark et al. 2013c). High-pitched sounds produced by flutter can superficially resemble whistles, but flutter can also produce low-pitched and buzzing sounds akin to the flight sound of a bee (Clark et al. 2011, 2013a).

Aeroelastic flutter lends itself to interspecific acoustic diversity, as small changes of feather shape produce differences in pitch, amplitude, and harmonic structure. Flutter-induced sounds are often not especially loud, but in some cases can carry for 100 m or more, apparently due to amplification mechanisms described later in this section. The shape of the sound field of fluttering feathers has not been measured, but the nature of the feather motion implies that it is a dipole, suggesting these sounds have strong directionality (Clark et al. 2013a).

Work thus far suggests that all flight feathers may spontaneously flutter under the right aerodynamic conditions, because flutter is a passive mechanism intrinsic to flat airfoils in fast flowing fluid (Clark et al. 2011, 2013a, b). Most individual feathers, tested in a wind tunnel, have many more possible modes of flutter than tend to be expressed in the flight of birds. That flutter occurs spontaneously demonstrates why this type of sound production could evolve easily. Experiments on living snipe and snipe feathers (*Gallinago* and *Coenocorypha* spp.) have demonstrated that flutter is responsible for the winnowing sounds they produce (Reddig 1978; Miskelly 1990).

Research on the mechanics of flutter has focused on single, isolated feathers mounted in a wind tunnel, because this is a tractable experimental paradigm. However, nearly all birds that produce sound with flutter have multiple neighboring feathers, making feather–feather interactions a possibility. In Anna’s hummingbird, the outer tail feather (R5) produces an approximately 4 kHz sound during a courtship display (Clark and Feo 2008). Its proximal neighbor (R4) does not produce this sound on its own, but the presence of R4 amplifies the sound produced by R5 by roughly 12 dB (Fig. 4.2). This interaction is not structural, because the effect can be produced when the neighboring feathers do not physically touch, so it thus must be an aerodynamically driven sympathetic vibration (Fig. 4.2d, e; Clark et al. 2011). It seems possible that this type of interaction is widespread in bird sonations, because amplitude (loudness) is a variable of paramount importance for communication. Another type of feather–feather interaction occurs when two neighboring feathers flutter at different frequencies, f_1 and f_2 . If the feathers are coupled, heterodyne (sideband) interactions appear at $f_1 \pm f_2$. This occurs in Allen’s Hummingbird (Clark et al. 2011; Clark 2014). In this species the tail feathers R3 produces f_1 (~2 kHz), while R4 produces f_2 (e.g., 7 kHz). When the two feathers are together, interaction frequencies of $f_1 \pm f_2$ (5 kHz, 9 kHz) appear as well. A third type of feather–feather interaction was demonstrated in Calliope hummingbird (*Selasphorus calliope*), in which flutter-induced collisions between neighboring fluttering feathers produce an atonal, buzzing sound (Clark 2011), discussed further in Sect. 4.2.5.

In addition to flutter, there are additional unidentified aeroacoustic mechanisms that apply to animals. The sounds produced by ruffed grouse (*Bonasa umbellus*) are made as the male beats his wings against the air with no physical contact between wings and another structure. The resulting low-frequency atonal pulses of sound carry hundreds of meters (Archibald 1974). The aeroacoustic basis of this sound has not been established. It could be simply due to direct pressure changes caused by dynamic motion of the wings; whether this mechanism alone can account for the

amplitude of the sound is unclear. As an alternative, the wings might force air out of the space between the wings and body to a degree sufficient to produce additional sound (see clapping, Sect. 4.2.5).

Even less clear is the physical basis of wing whirring wing sounds produced by birds such as toadies (Todidae) and manakins in the genera *Pipra* and *Manacus* (Fig. 4.1; Bostwick and Prum 2003), for which the acoustic mechanism remains unknown. One mechanism that obviously does not apply to living vertebrates is a sonic boom, as produces the crack of a bullwhip (Bostwick and Prum 2003). This mechanism requires local velocity of some part of the animal to exceed c (~ 340 m s^{-1} in air), a velocity many times higher than the fastest speeds of any animal or animal appendage, although it is plausible the tails of sauropod dinosaurs could reach it (Myhrvold and Currie 1997).

The aerodynamic mechanisms described in the preceding paragraphs produce significant levels of sound only at high speeds, mostly above 10 m s^{-1} in air. A hovering or slow-flying bird or bat flapping its wings has local wingtip velocities of approximately 10 m s^{-1} , which is why all flying vertebrates produce one or more of the previously mentioned acoustic signatures in flight. Most of these aerodynamic mechanisms are unimportant for terrestrial locomotion, owing to low velocity. For terrestrial animals it is instead interactions with a solid substrate, or at the air–water interface that tend to dominate their acoustic signatures.

4.2.5 Structural Mechanisms

Air is a nearly uniform medium, meaning that the aerodynamic sound production mechanisms described in Sect. 4.2.4 are dependent largely on the animal's morphology and kinematics. By contrast, many sounds of terrestrial locomotion vary substantially with the local substrate. Everyday experience shows that the same human foot actuated under similar kinematics produces different sounds when walking on snow, leaf litter, through dry grass, or through mud, on account of differences in the physical interactions of the foot with each of these substrates.

When two solid objects collide, rub, or otherwise move relative to each other, the result is local structural deformations and vibrations. Mechanisms generating vibrations include collision (percussion), rubbing (stick-and-slip), sudden material failure (as in a stick snapping underfoot), or other physical interactions between the two structures. Structural vibrations induced by physical contact produce airborne sound, because a surface vibration of a solid structure produces an equivalent vibration in the layer of air attached to the surface. This is due to the no-slip condition, in which the layer of air that is in contact with a solid at the solid–air interface moves along with the solid; the two do not slip relative to each other (Vogel 1994).

The proximity of two solid objects can also induce forced air movement. If air becomes trapped (restricted) between two moving objects, local pressures can briefly rise greatly, resulting in a significant amount of additional sound. For instance, clapping hands causes sound not by percussion-induced vibrations of the skin, but from shockwaves associated with air forced out from between the two

hands. This is easy to demonstrate by observing how the sound of clapping changes with how the hands are cupped: Cupping affects the volume of air and local geometry of how the air is forced out (Fletcher 2013).

There appears to be high mechanistic diversity of how structural sounds may be produced, and no conceptual overview of all of the ways animal motions generate structural sounds. This may be a fruitful avenue for future research and synthesis. For the remainder of this section, attention is focused on recent research on how manakins and hummingbirds produce sounds via interacting solid structures.

Male manakins (Pipridae) are lekking birds that defend small courts and perform athletic displays for females. Many species produce sonations, particularly snapping sounds but also including other mechanisms (Fig. 4.1) (Prum 1998; Bostwick and Prum 2003, 2005). Snaps are percussive, produced by abrupt, impulsive physical contact between a wing and another structure, including the other wing, the body, or between individual wing feathers within a wing (*click* sounds of *Pipra mentalis*). The sounds produced are sudden, short, broadband impulses of sound, (Bostwick and Prum 2003). Male manakins have thickened wing feather shafts and enlarged, sexually dimorphic muscles associated with these displays (Schultz et al. 2001).

Instead of a strictly percussive mechanism of sound production, the club-winged manakin (*Machaeropterus deliciosus*) uses stridulation to produce pure tones with its secondary wing feathers (Bostwick and Prum 2005; Bostwick et al. 2009, 2012). Males elevate the wings over their back, and then rapidly, repeatedly collide the medial secondary feathers of the opposing wings together. The fifth secondary wing feather (S5) is a pick, S6 is a file, and the two together produce loud tonal sound with a fundamental frequency of 1.5 kHz (Fig. 4.4).

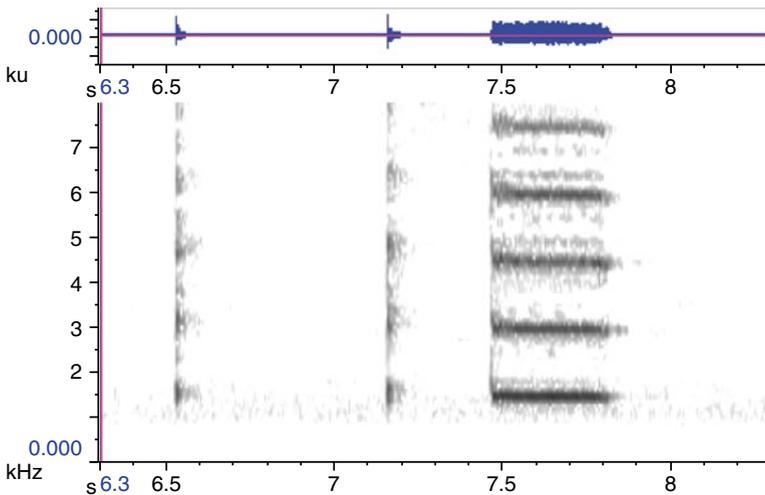


Fig. 4.4 Spectrogram and waveform of sonation of club-winged manakin (*Machaeropterus deliciosus*), produced by wing stridulation. Recording from Xeno-Canto #213391

This physical source of sound is augmented by two additional mechanisms that amplify amplitude. First, the wing feathers are stiff and, in comparison to wing feathers of other manakin species, have resonance frequencies tuned to 1.5 kHz. Neighboring feathers vibrate coherently and in phase, as indicated by their response to mechanical stimulation. This means the feathers of one wing are undamped and act as a functional unit, ringing collectively in response to the input frequency of the pick and file (Bostwick et al. 2009). Second, the ulna, the bone into which these secondary feathers insert, is robust and densely mineralized (Bostwick et al. 2012). This implies that its structural properties are also tuned for sound production. The precise role the ulna plays in sound production is unclear. It provides a solid, dense attachment point for the secondary feathers, stronger than in typical passerines. It may serve as a node (like the handle of a tuning fork), modulating the vibration of neighboring wing feathers while structurally isolating them from the rest of the bird, reducing damping of the feathers and thereby increasing the amplitude of the sound (Bostwick et al. 2012).

One final physical acoustic question not yet addressed is whether there is a phase-inverting mechanism between the wings, similar to stridulatory mechanisms in crickets (Bennet-Clark 1999). Without such a mechanism, when the two wings are struck together, they may vibrate in antiphase (a phase offset of 180°) relative to each other, causing destructive interference between the two wings, thereby reducing the amplitude of the sound. But that such a mechanism is needed is not entirely clear, as the two wings are held approximately coplanar when the bird sonates, and so might already have axes of vibration rotated 90° relative to the input impulses. One way to test this may be to examine the shape of the sound field around a sonating manakin.

Another mechanism that appears to be widespread in terrestrial vertebrates is rubbing or rustling, as in the sounds apparently produced by the modified hairs of streaked tenrec (Endo et al. 2010). Multiple physical mechanisms seem plausible explanations of such sounds, such as from stick-and-slip friction of two surfaces in contact. Feathers rubbing against feathers appear to produce *fanning* sonations in manakins in the genus *Manacus* (Bostwick and Prum 2003), and seem to be widespread in other birds, such as in adventitious sounds of wing and tail feathers rubbing against each other as a bird preens itself.

In addition to the wings and tail, the head, bill, and feet of animals also serve as percussive instruments. Woodpeckers drum with their bill adventitiously when foraging, but also seek out resonant surfaces to amplify loudness, and drum as a sonation to declare a territory (Stark et al. 1998). Ruddy ducks (*Oxyura jamaicensis*) thump their bill against their upper breast, producing an accelerating train of dull, quiet *thuds* in a close-range courtship display (Clark, pers. obs.). Many mammals drum, striking the ground with their feet or other parts of the body (Randall 2001), signals that may transmit vibrationally as well as acoustically.

A structural mechanism mentioned in Sect. 4.2.3 involves flutter-induced collisions. Male Calliope hummingbirds produce a strange buzzing sound with a dominant frequency of approximately 1 kHz, and modulated in pulses at 0.25 kHz,

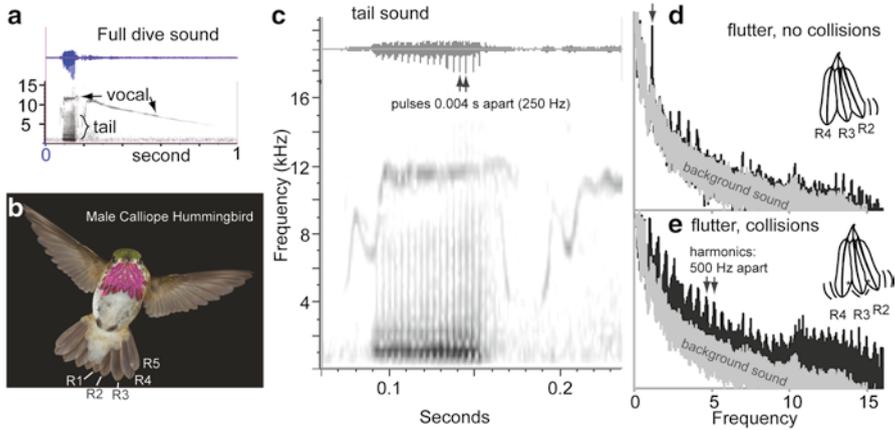


Fig. 4.5 Dive sound of male calliope hummingbird (*Selasphorus calliope*) includes sound produced by tail feathers fluttering and colliding with each other. **(a)** Dive sound includes both vocal and tail-generated elements. **(b)** Adult male calliope hummingbird with sound-producing tail feathers (rectrices, R1–R5) indicated. **(c)** Tail-generated portion of the sound recorded at 24 kHz, FFT: Hann, 50 % overlap, window size of 128 samples to emphasize the time domain. **(d, e)** Wind tunnel experiments to reproduce acoustic mechanism, in which three tail feathers were mounted adjacent to each other, in an orientation similar to that observed in the bird. *Black* is spectrum of interest, *gray* is the background noise of the wind tunnel with feathers present but not fluttering. **(d)** One or more feathers fluttered but did not collide, replicating only the approximately 1 kHz fundamental frequency of the dive sound (*arrow*), and not the acoustic energy greater than 1 kHz in the dive sound. **(e)** Feathers fluttered and collided at approximately 0.5 kHz, resulting in energy transfer to higher frequencies, replicating the acoustic structure observed in the dive sound. Power spectra of **d, e** produced in Raven 1.4 with a 65,536 FFT sample window [Modified from Clark (2011). Wing, tail, and vocal contributions to the complex acoustic signals of courting Calliope hummingbirds. *Current Zoology*, 57, 187–196. Reprinted with permission from the editorial office, *Current Zoology*]

during their courtship dive (Fig. 4.5). Unlike in relatives, removing single tail feathers had small effects on the buzzing sound, whereas removing the entire tail eliminated this sound. This implied that the source was the tail feathers as a group, rather than individual feathers (Clark 2011). Single tail feathers tested in a wind tunnel produced little sound, and had an easily elicited torsional mode at 0.5 kHz (Clark 2011; Clark et al. 2011). When sets of three tail feathers were tested together, this torsional mode seemed to facilitate collisions between neighboring feathers. These feather–feather collisions produced a buzzing sound rich in harmonics, similar to the dive sound (Fig. 4.5e) (Clark 2011).

Many other birds are reported to have multiple neighboring feathers with modified shape that may interact (Trail and Donahue 1991; Lane et al. 2007), especially guans (Delacour and Amadon 1973). Whether these other taxa also have similar, aerodynamically driven structural sound production mechanisms remains to be seen.

4.2.6 Source-Filter Theory

Closely related species may evolve acoustic differences in their sonations, as has happened in hummingbirds, snipe, or manakins (Prum 1998; Clark 2014). Because the physical mechanism that produces the sound is accessible to subtle manipulations, relatively nuanced hypotheses of how the source generates sound can be developed and tested. Many hummingbirds studied have multiple unusually shaped tail feathers, and yet experiments demonstrate only some of these feathers were necessary and sufficient for sound production. Other feathers with noteworthy shapes, generally neighbors of the necessary and sufficient feather, were not themselves necessary or sufficient. A vibrating feather may aerodynamically interact with its immediate neighbors, acting as coupled oscillators (Sect. 4.2.3), and complex interactions between individual feathers are physically plausible in most birds that produce sound via flutter. To provide a theoretical framework for understanding these complex interactions and how they evolve, Clark (2014) proposed a source-filter model of sonations that he applied to the evolution of sonations generated by the tail in hummingbirds in the genus *Selasphorus*.

The sound source is defined as the minimum set of structures both necessary and sufficient to produce quantifiable components of the sound of interest (see Sect. 4.2.2), while filters are adjacent structures to which the source is plausibly coupled, either structurally or aerodynamically. In the simplest cases, one single individual feather (or feather region) was both necessary and sufficient for sound production, making that feather the only source and a “lynchpin” for sound production (Table 1 in Clark 2014). This lynchpin model does not apply to all species: in Calliope hummingbirds, the tail feathers in aggregate are the source (Fig. 4.5).

Filters are by themselves unnecessary and/or insufficient for production of *quantifiable* components of sound, where amplitude and aspects of timbre are hard to quantify, particularly in the field. Because they by definition lack evidence of being the source, filters are always hypothetical in a particular species. As they may vibrate in forced response to a neighboring source feather to which they are coupled, and are presumably evolutionarily tuned to do so, this model predicts that filters are prone, over evolutionary time, to become sources. Moreover, filters could be spectral filters, for instance amplifying only some of the bandwidth of a source, such as a harmonic higher than the fundamental. As such, the model predicts that sonations could switch over evolutionary time from one frequency to another by hopping from one harmonic to another. This model explains patterns of evolution of mechanical sounds within the hummingbird genus *Selasphorus*. The ancestral character state is to produce a sound at approximately 1 kHz + integer harmonics by feather R2 source, and has evolved to a 2 kHz + integer harmonics sound from an R3 source in Allen’s hummingbird. This could not have been the result of small, gradual changes from 1 to 2 kHz as the source shifted from R2 to R3, because Allen’s R2 still has the ancestral character state, a “ghost” fundamental frequency of approximately 1 kHz, that is expressed when feather R3 is missing (Clark 2014). Therefore the simplest explanation is that the dominant frequency has “hopped” from the fundamental frequency of R2 to the second harmonic, which became the

new fundamental frequency of R3, a process termed “harmonic hopping” (Kingston and Rossiter 2004; Robillard et al. 2013). This model provides a mechanism of how fundamental frequency of communication sounds can hop from one discrete frequency to another, a topic discussed further in Sect. 4.3.4.

This source-filter model should not be confused with the source-filter model of vocalizations (see Taylor et al., Chap. 8). As discussed in Sect. 4.4.1, animals seem to have greater control over the acoustic form of vocalizations than over nonvocal sounds. In the source-filter model of vocalizations, source and filter are also coupled, but animals control mechanical properties of the filter independently of the source, resulting in much of the diversity of the acoustic form of vocalizations. The source-filter model of sonations, by contrast, invokes no evidence of independent control of the filter. Rather, the model is a tool to understand how mechanical sounds evolve, in the context of experiments that show that a particular structure is either not necessary or insufficient for sound production in a particular species, yet phylogenetic evidence implies that such structures have played a role in sound production in the past and in sister taxa.

4.3 Function and Behavioral Significance

Both sonations and adventitious sounds play important roles in the biology of locomotion. Locomotion-induced sounds may alert individuals to the presence of an animal and its motions (Randall 2001). In addition to their role in communication, these sounds also play roles in predator–prey interactions. Owls can successfully capture prey in total darkness, using only the adventitious sounds of locomotion of prey (Konishi 1973). One widespread response of prey to a potential predator is to freeze, thereby ceasing production of locomotion-generated sound. Similarly, one hypothesis for the silent flight of owls is that reduction of self-noise masks from the prey the sound of the owl’s approach (Konishi 1973). This section hereafter ignores predator–prey interactions and acoustic stealth and focuses on how sonations attain communication function.

Sonations appear to serve all of the same communication functions that vocalizations do, including as alarms for conspecifics, such as rodent thumping (Randall 2001) or dove flight sounds (Hingee and Magrath 2009); as aposomatic warnings (rattlesnake rattles), in territorial advertisement in place of undirected vocal song (ruffed grouse, broadbills in the genus *Smithornis*), and during displays directed toward conspecifics, as in manakins or hummingbirds. Vocal morphology seems to have arisen relatively few times in ancient lineages, providing a limited phylogenetic sample size with which to seek inferences as to why vocal acoustic communication originally evolved. By contrast, many sonations have evolved recently, yielding at least hundreds of independent phylogenetic origins of these behaviors. In bird sonations produced with the wings and tail, the majority of these types of sonations arise as sexual behaviors produced predominantly by one sex (usually males), either in place of vocal song, or during courtship displays directed at females (Clark, pers. obs.).

4.3.1 Kinematics Revisited: Animal Behavior

Section 4.2.1 explored the relationship between animal kinematics and sound from an experimental point of view, including discussion of whether these sounds are voluntary. This section turns to how the relationship between sound and motion influences the potential information content that nonvocal behaviors contain. The direct correspondence between motion and locomotion-induced sound (Sect. 4.2.1) has a key implication for animal behavior: Locomotion-induced sounds intrinsically contain information about the animal and its movement. The sound is a physical record of the behavior. Locomotion-induced sounds are not arbitrary in form, as vocal songs (especially learned songs) may be; they are physically constrained by the motions that produce them.

Timing variables seem likely to be especially effectively encoded acoustically. Perhaps they are easier for a receiver to evaluate accurately and precisely than even visual observation of the same behavior. Sound is an acoustic record of repeated motions, particularly for events measured in the time domain of a spectrogram. For instance, the wingbeat frequencies of displaying hummingbirds, manakins, or flappet larks (*Mirafra cinnamomea*) are nearly doubled during production of sonations (Norberg 1991; Bostwick and Prum 2003; Feo and Clark 2010). This change in frequency is easily heard or measured in a spectrogram (Fig. 4.6a, b). Although it has not yet been demonstrated that females pay attention to the wingbeat frequency of courting males in species such as these, this seems likely. Playback experiments show that hummingbirds respond to and use the wing sounds to identify the species/sex of other individuals (Hunter and Picman 2005; Hunter 2008).

In crested pigeons, Hingee and Magrath (2009) used playback experiments to demonstrate that the wing sound of a pigeon taking off normally did not elicit a response from a flock of pigeons (Fig. 4.6a), but playing back the wing sounds of a

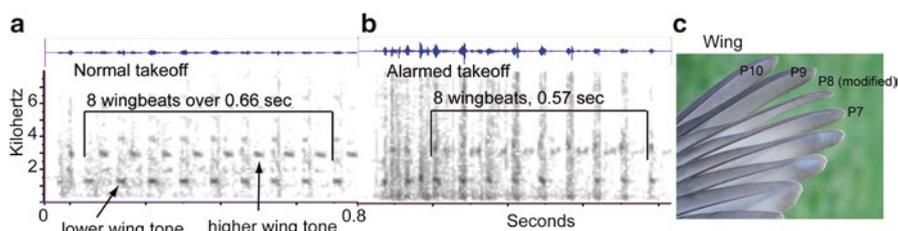


Fig. 4.6 Wing sounds produced by crested pigeon (*Ocyphaps lophotes*) during normal takeoff, alarmed takeoff, and wing showing modified primary feather P8. (a) During flight, this species produces two temporally offset sounds, lower and higher wing tone. The lower tone is likely produced during the downstroke. In normal takeoff this bird had a wingbeat frequency of 12.1 Hz ($8/0.66$), whereas in alarmed takeoff (b) the wingbeat frequency was 14 Hz ($8/0.57$). Hingee and Magrath (2009) demonstrated that pigeons flee in alarm to this higher wingbeat frequency, and not the lower frequency of ordinary takeoff. (c) The wing has a modified feather, P8, which is narrowed and stiffened, apparently for sound production of some or all of the wing sound. Sounds courtesy of Trevor Murray, photo of specimen 5653 from the Australian National Wildlife Collection, courtesy Robert Magrath. FFT: 512 samples; Hann, 50 % overlap (44 kHz)

bird taking off in alarm, with wingbeat frequency at a slightly higher tempo (Fig. 4.6b), caused the whole flock to take off in response. Further playback experiments demonstrated that this effect was not attributable to differences in the sound's amplitude. This result implies that the birds responded to the increase in wingbeat frequency. This simple experiment shows crested pigeons listen to each other and that the wing sounds serve as an alarm signal. Because the sound pulses are produced directly by the wingbeat, they are not susceptible to cheating, unlike vocalizations, although if they are under voluntary control (Sect. 4.2.1.1) the animal might choose not to produce the sound.

Beyond time-domain variables, additional information may be encoded by a sonation, such as sound features often measured in the frequency domain. What information frequency-domain variables contain depends on the particular physical mechanism producing the sound. In the case of flutter-induced sounds generated by feathers (e.g., hummingbird tail feathers), the pitch in many species encodes information about the signaler's flight velocity. In many feathers, amplitude and pitch of flutter-induced sound both change systematically with speed (Clark et al. 2011). But as the slopes of these relationships varied substantially among species tested (Clark et al. 2013b, c), data from one species cannot be readily extrapolated to another.

4.3.2 *Relationship with Displays*

Darwin (1871) was the first to observe that vigorous courtship displays may lend themselves to sonations, stating:

We have seen that some birds during courtship flutter, shake or rattle their unmodified feathers together; and if the females were led to select the best performers, the males which possessed the strongest or thickest or most attenuated feathers, situated on any part of the body, would be the most successful; and thus by slow degrees the feathers might be modified to any extent. The females... would not notice the slight successive alternation in shape, but only the sounds thus produced. (Chap. XIII, p. 67)

Two factors may promote sonations arising during displays rather than other social contexts. First, displays are often vigorous, involving rapid appendage movements, and thereby tend to incidentally produce more adventitious sound than more placid movements. Second, if receivers are attuned to subtle differences in display performance, it may be relatively easy for female preferences to switch to male attributes that contain information about these differences. There is not yet evidence for which of these two factors may play a larger role in driving the evolution of new acoustic communication systems.

The coupling of sound to motion means that information about locomotion itself is intrinsically contained in locomotion-induced sound. This makes sonations a likely sensory modality for direct assessment of a locomotor performance of another individual. In courtship displays, females might evaluate subtle differences between males against poorly understood performance criteria. Aspects of these performance criteria, whatever they are, may be more efficiently transmitted or perceived

acoustically than visually. For instance, suppose female auditory systems encode temporal frequency more precisely than visual systems (Sect. 4.3.1): If so, attention to acoustic characters of displays may allow finer discrimination between male performances than would visual observation of the same display. This is true regardless of the adaptive value of female preferences, that is, regardless of whether one believes females derive useful information from “honest” signaling on the part of the male, or whether female preferences are arbitrary (Prum 2010).

4.3.3 *Relationship with Vocalizations*

There is limited evidence in birds that vocalizations and sonations trade off, with sonations apparently replacing vocalizations. In *Pseudocolaptes* flycatchers, Bostwick and Zyskowski (2001) document closely related taxa, some of which produce a regular vocalization, others of which have replaced the sound with a bill snap. Ruffed grouse produce sonations that are the functional equivalent of vocal song, and also lack vocal songs, as do *Smithornis* broadbills (Clark, pers. obs.). These taxa have reduced syringes (Prum 1993) and reduced vocal capacity (Rusch et al. 2000). Species such as vultures or mute swan (*Cygnus olor*) are relatively nonvocal and produce distinctive flight sounds, but it has not been established whether their distinctive sounds are sonations that have replaced a vocal function, or are simply adventitious. It also has not been established whether the examples just provided are rare exceptions or the general rule, and this could be tested phylogenetically. As evidence against this tradeoff hypothesis, a number of taxa that produce sonations are also highly vocal, such as Anna’s hummingbird, or humans. Perhaps vocalizations and sonations trade off only in specific evolutionary contexts.

Another pattern observed in hummingbirds is similarity between phonations and sonations. Costa’s and Anna’s hummingbirds both have strong intraspecific similarities between their vocal songs and nonvocal dive sounds, but larger interspecific differences (Clark and Feo 2010). The most parsimonious phylogenetic reconstruction has in their ancestor a single similar song and dive sound, which have each diverged in the daughter taxa. What selective force would maintain two mechanisms of sound production that yield similar sounding sounds? Clark and Feo (2010) propose that a similar female preference selects for similar acoustic form via “sexual sensory bias,” but a key prediction of this hypothesis, that females do prefer the similar components of sound in each display, has not yet been tested.

No other published examples of self-imitation between vocalizations and mechanical sounds are yet known, but additional instances could be easily overlooked. Baptista and Matsui (1979) concluded that the dive sounds of Anna’s and Costa’s hummingbirds were vocal because they sounded just like the obviously vocal song (Sect. 4.2.2). This argument is normally a reasonable one. If an animal produces two similar sounding sounds, the null hypothesis is that they are simply serial repetitions of the same signal. It takes specific, positive evidence to the contrary to conclude that two similar sounds in fact constitute different signals (Clark and Feo 2010).

4.3.4 Evolution

Communication sounds arise out of adventitious sounds that become salient to receivers (Darwin 1871; Ewing 1989). Once signaler–receiver coevolution begins, the signal may become modified in form, for instance, becoming louder or changing in pitch. It seems that many sonations are quiet, and perhaps there are fewer options for evolution to modify external animal morphology to add resonators or other mechanisms that amplify acoustic amplitude, than are available for vocal mechanisms. What is clear is that, just as Darwin (1871) hypothesized, subtle changes in morphology can have significant impacts on acoustic form (Clark et al. 2011). In the case of feathers and aeroelastic flutter, these sounds may evolve in either a linear or nonlinear fashion.

It is easy to imagine the linear case: over evolutionary time, a slight, gradual change in morphology of a resonator changes stiffness, and that produces a slight, gradual change in pitch. For instance, a slightly stiffer feather produces a slightly higher pitch. However, pitch may also evolve nonlinearly, jumping abruptly from one frequency to another. One example of how this can occur was described in Sect. 4.2.6. There is a second way, and it occurs because three dimensional resonant structures have multiple resonance frequencies that are not integer multiples. Changes in how the structure is excited can cause the system to cross a threshold, transferring excitation from one resonance frequency to another (Clark et al. 2012). The result is that, when such a threshold is crossed, the system may “jump” from one vibration frequency to a much different one. The difference between this mechanism and the one described in Sect. 4.2.6, is that this mechanism concerns frequency jumps *within* a single feather, whereas Sect. 4.2.6 described a switch *between* coupled adjacent feathers. It is trivial to make feathers fluttering in a wind tunnel (under artificial conditions) jump from one mode of vibration to another. A natural example is shown in Fig. 4.2c, of an Anna’s hummingbird dive sound. The dive sound contains a prominent approximately 1.2 kHz sound that is produced by a tip mode of vibration, just before and after the typical approximately 4 kHz trailing vane mode (Clark et al. 2013a). Evolutionary changes in morphology may produce both linear and nonlinear changes in the types of sound produced. And to extend the analogy raised in Sect. 4.2, these constitute changes in the instrument itself.

The other major way sonations may vary among related taxa is behavioral, in “how the instrument is played.” Manakins produce either single snaps, or “roll-snaps” that consist of a rapid-fire sequence of snaps. In either display, the physical acoustic mechanism is the same, differences in acoustic form arise from behavior. Woodpeckers (Stark et al. 1998) and various mammals (Randall 2001) drum using the same percussive mechanism, but behaviorally produce species-specific sequences. Hummingbirds produce a diverse array of sounds with their wings and tail, where evolutionary diversity in the form of the sound arises from changes both in morphology and in behavior; tail feather shape changes the pitch, amplitude, and harmonic structure of sound, while behaviorally the birds vary in the number and duration of pulses of sound that are produced by spreading the tail (Clark and Feo

2010; Clark et al. 2011). Whether sonations evolve more under the action of changes in the instrument (morphology), or changes in playing style (behavior), remains to be tested.

4.4 Limitations and Advantages

Sonations seem to evolve repeatedly and recently in comparison to the ancient origins of vocalizations deep in the vertebrate phylogeny. Though sonations may be produced by any part of the animal, and are therefore arguably morphologically more diverse than vocalizations, it seems they are acoustically less diverse than vocalizations. This is apparently due to the inflexible nature of the sound production mechanisms underlying many sonations. A key innovation of vocalizations, poorly replicated by sonations, is the ability for the acoustic form to be dynamically and actively modulated by the animal, both within the source (larynx/syrinx) and filter (vocal tract) (Taylor et al., Chap. 8). The inflexibility of sonations is also a potential advantage in some contexts, as it allows sonations to contain information about locomotion and performance that is not intrinsic to vocalizations, which have greater potential to be arbitrary in acoustic form.

4.4.1 *Physical Limitations*

A feature of birdsong is biphonation, two-voiced song, via production of two independent sounds on each side of the syrinx. By doubling the number of sounds that can be produced at any moment, biphonation greatly increases the diversity and complexity of bird vocalizations relative to other animals (Riede et al. 2006; Zeigler and Marler 2012). In this respect, sonations could be even more diverse, because the number of simultaneous sounds an animal can make is limited only by the number of appendages it has. For instance, a human acting as a “one-man band” can make several sounds at once, including clapping hands, stomping feet, and head motions. Allen’s hummingbirds trisonate (produce three nonvocal sounds at once) during their dive, simultaneously producing one sound with the wings and another two with the tail (Clark et al. 2011). A number of other hummingbirds produce sounds with both wings and tail during display (Feo and Clark 2010), or coordinate vocal and nonvocal sounds. However, even though there are more possible sonations than phonations, claims such as that Allen’s hummingbirds trisonate (Clark et al. 2011) are a bit superficial. The reason is that locomotion-induced sounds remain less acoustically diverse than vocalizations because they are not as subject to modulation as are vocalizations.

Sonations are less subject to modulation than vocalizations in two respects: Acoustically they are relatively fixed in form, and behaviorally there are fewer options available for them to be voluntary, produced independently of other behaviors such as

locomotion. Intrinsic aspects of the sound production mechanisms (Sect. 4.2) limit the acoustic form of sonations. For instance, consider frequency. Many sonations, such as a hummingbird's wing trill, contain two frequencies—a higher frequency set by a mechanism such as flutter of individual wing feathers (usually measured in the frequency domain), and the lower pulse rate (usually measured in the time domain) set by the oscillation of the wing. One pulse of sound is produced by each flap of the wing. Both the higher frequency and the lower pulse rate are relatively fixed; the pulse rate is fixed by the muscular and other mechanical limitations of the limb, similar to how vocal trill frequencies are limited by the vocal tract, such as in Darwin's finches (Podos 2001; Podos et al. 2004). The higher frequency is limited by the mechanics of flutter, and in most cases flutter of a particular feather produces only a narrow frequency range, often varying by less than 20 %. As a result of these constraints, wing trills of any particular species do not and likely cannot express the same frequency range observed in the trilled vocalizations of passerine birds.

Some frequency modulation is possible. The highest known *potential* frequency modulation of a sonation is from *Chaetocercus* woodstars. In a wind tunnel, their tail feathers can vary in frequency by roughly 50 %, through changing the orientation of a tail feather relative to airflow (Clark et al. 2011, 2013b). The degree to which birds take advantage of this entire range of motion is unclear. While *Chaetocercus* tail feathers can change pitch through changes in feather orientation relative to airflow, most taxa modulate these sounds via changing flight speed during a dive such as in Costa's hummingbird (Clark and Feo 2010) or snipe (Reddig 1978). This means they are frequency modulated by the animal only with physical difficulty, and in only one behavioral context, diving. Greater sage grouse produces an FM swish during its display as the wings are brushed against stiff breast feathers (Koch et al. 2015). By comparison, vocalizations are acoustically more diverse because animals change pitch of vocalizations rapidly and easily via either vocal source or filter (Düring and Elemans, Chap. 5; Taylor et al., Chap. 8).

Beyond frequency, two additional acoustic parameters that could pose limitations on the form of sonations are intensity (amplitude) and directionality, though rigorous data are scarce. The only amplitude data are from ruffed grouse, with sound pressure levels (SPLs) at a reference distance of 1 m of 64–70 dB (Garcia et al. 2012b). Many of the best-known sonations (snipe winnowing, Anna's hummingbird tail sound, manakin wing snaps) can carry for 100 m or more under natural ambient conditions; lyre-tailed honeyguide (*Melichneutes robustus*) tail sounds and ruffed grouse wing sounds are audible several hundred meters away (Friedmann 1955). These sonations approach or exceed (Clark and Feo 2008) the loudness of similar vertebrate vocalizations—but these examples may also be exceptions, studied or well-described specifically because of how loud they are. Ordinary adventitious sounds are often quiet, and the problem of diagnosing sonations versus adventitious sounds (Sect. 4.2.1) renders problematic any assertion about the average amplitude of sonations, owing to intrinsically arbitrary decisions about which quiet sounds to include in such an analysis.

Acoustic directionality of sonations has been studied only in ruffed grouse (Archibald 1974; Garcia et al. 2012b). Garcia et al. (2012b) found that acoustic

radiation from ruffed grouse is similar to a dipole, with nearly equal SPL levels directly in front of and directly behind the drumming bird, but significantly lower SPL to the sides. Because sonations are produced external to the animal, sonating animals may have fewer physical avenues available for beaming the sound in a single direction, as compared to vocalizations. Several of the mechanisms outlined in Sects. 4.2.3 and 4.2.4 seem likely to be inherently dipole like.

4.4.2 Behavioral Limitations

In addition to acoustic limitations, sonations may also be behaviorally limited. The animal must perform a discrete, obvious behavior to produce the sound. That this is a limitation is situational; this same feature is also an advantage (see Sect. 4.4.3) in different circumstances. Birds that broadcast undirected sonations in place of vocal song, for instance, tend to perch in one place and then either jump, or flap the wings vigorously, to produce sound. If visual crypsis is important, such as to avoid predators, a sonation will be at a relative disadvantage to a vocalization. Further, the sounds can be difficult for the animal to modulate strategically. Hingee and Magrath (2009) demonstrated that crested pigeons use the wing sounds of other individuals as an alarm signal, because, when alarmed, pigeons flap their wings at an audibly higher rate. Unlike an alarm vocalization, it is not possible for a crested pigeon to strategically signal alarm without taking flight; and they may also not have the capacity to strategically choose to flee silently, if this were advantageous.

Finally, a limit sometimes invoked is the “energetic cost” of vigorous displays that accompany some types of sonations (Clark 2012). The performance of a behavior that produces a sonation could result in energy costs that exceed the costs of a similar vocalization. But because energy costs scale with the time duration spent performing the behavior (Clark 2012), most if not all individual sonations cost only small to trivial amounts of energy relative to an animal’s daily energy budget. For instance, Barske et al. (2014) placed heart rate monitors on golden-collared manakins (*Manacus vitellinus*) to document heart rate during display, which includes production of wingsnap and rollsnap sonations. Though heart rate during display was high, display only occupied approximately 5 min/day and accounted for only 1.2 % of the daily energy budget. Animals that produce sonations repeatedly throughout the day (such as ruffed grouse) may entail nontrivial energy costs, if the total amount of time spent performing the behavior is significant. As ruffed grouse produce sonations when otherwise sitting still, it might be possible to examine directly how much energy production of sonations cost. But for many species, such as manakins, it may be difficult to differentiate between calories expended producing a sonation, versus other vigorous components of display, because the two are performed at the same time. Regardless, there is no evidence or theoretical reason to believe that sonations consume any more than a trivial amount of energy, because most sonations are produced infrequently (Clark 2012).

4.4.3 *Advantages*

This 1:1 link between motions and sound, described in Sect. 4.4.1 as a limitation, is also an advantage in other ecological circumstances. As described in Sect. 4.3.1, the intrinsic link between kinematics and sound makes sonations an acoustic record of an animal's performance of a behavior. In some communication contexts such as courtship displays, it is thought that the quality of a performance is important to females (Byers et al. 2010). The 1:1 correspondence between motion and sound means that sonations are intrinsically suited to be index signals of performance quality because they are an acoustic record of the performance itself. For instance, a wing trill encodes wingbeat frequency (Sect. 4.3.1). Sound may be the better sensory modality for a female to evaluate locomotor variables such as frequency. To a human, the increase in wingbeat frequency of displaying hummingbirds is difficult to discern visually, as their normal wingbeat frequencies are above the human flicker–fusion frequency. Yet increases in frequency associated with displays are easy to detect by ear. Acoustic evaluation of displays may afford females the best ability to make subtle discriminations between potential mates, a hypothesis that has not yet been evaluated for any sonating species.

Another advantage of locomotion-induced sounds is experimental: sound of a behavior can be easier to record than video, so locomotion-induced sounds may be useful for studying locomotor performance and behavior. As described in Sect. 4.2.2, the sound production morphology is external to the animal, making experimental manipulations that affect the sound production mechanism especially feasible in some animals. Such experimental manipulations allow experimental tests of acoustic function, in ecologically relevant contexts, in ways largely unavailable to students of vocalizations.

4.5 Summary

Mechanisms of locomotion-induced sounds are diverse (Bostwick 2006). All locomotion produces sound via several possible physical acoustic mechanisms. Therefore locomotion-induced sound is an intrinsic component of virtually all animal behavior, though some locomotion produces so little sound as to be effectively silent. Locomotion-induced sounds tend to be loudest during rapid or vigorous behaviors, such as displays. These sounds can evolve from adventitious sounds that are an incidental byproduct of motion into communication signals called sonations. Because locomotion-induced sound is ubiquitous, sonations have evolved independently out of adventitious sounds repeatedly, particularly during displays (Fig. 4.1).

Mechanistically, production of sonations can be examined at the level of animal motions (kinematics) and the physical acoustic mechanism that generates sound. Air is a nearly uniform medium, so the acoustic form of flight sounds is dependent largely on an animal's morphology and kinematics. By contrast, many terrestrial

locomotion-induced sounds (such as footsteps) come from interactions between the animal and a substrate, meaning that substrate variability produces an array of possible sounds that could be produced by a particular morphology and kinematics. Physical acoustic mechanisms of locomotion-induced sounds are diverse, taxon specific, and poorly described, and can be divided into aerodynamic and structural mechanisms.

There is a direct correspondence between locomotion-induced sounds and an animal's motions. This correspondence has two implications. The first is experimental: Sound recordings of a behavior are a perhaps underutilized source of data about an animal locomotion, and sound recordings are easier to obtain than video in some contexts. With sufficient prior information, a sound recording yields information about locomotion. However, in diagnosing the relationship between kinematics and sound, beware of spurious correlations, when an obvious motion is correlated with but does not cause the sound (Fig. 4.3). The second implication is behavioral: The correspondence between behavior and sound means that the locomotion-induced sound contains information of potential use to other animals, especially by encoding frequencies, such as that of the wingbeat. Therefore, sonations are intrinsically suited to contain information about performance ability, suggesting the hypothesis that animals use sonations to evaluate locomotor performance.

It can be difficult to diagnose which locomotion-induced sounds are sonations and which are adventitious. The simplest diagnosis of a sonation is provided by morphology evolved specifically for sound production, such as the rattle of a rattlesnake. The second simplest diagnosis comes from kinematics specialized for sound production (rattlesnakes rattle their tail). When the animal lacks obviously specialized morphology or behavior, then the criterion is whether the sound is produced voluntarily. Voluntariness, the degree to which an animal modulates locomotion-induced sound independent of other behaviors, can be difficult to assess. Locomotion-induced sounds may be produced only in certain behavioral contexts, but this is not proof of voluntariness. The hidden switch hypothesis states that the sound is voluntary and is controlled via a switch that is subtle and not easily detected ("hidden" to casual observation); the null is that the sound is not voluntary. Support for the hidden switch hypothesis entails positively identifying the switch (which may be kinematic or morphological). This will often be hard to do, and so many potential sonations will be difficult to diagnose as such.

4.5.1 Avenues for Future Research

Decades of research on how vertebrates vocalize have chipped away at questions of vocal function and vocal mechanism. In comparison, sonations seem disproportionately understudied. The physical acoustics of sonations remains wide open for future research; surely not all possible mechanisms have been identified in Sects. 4.2.4 and 4.2.5, and some of the mechanisms qualitatively sketched in this review

are conjectural and warrant further empirical validation. At the same time, as some of the physical acoustic mechanisms seem likely to be specific to individual species or small clades, rather than broad or general, examination of physical acoustic mechanisms for their own sake may not be especially conceptually exciting.

Rather, physical acoustic mechanisms of sonations should be further studied because they have behavioral, ecological, or evolutionary implications. Understanding the physical mode of sound production reveals, for instance, that sound pitch can evolve both linearly and nonlinearly (Sects. 4.2.6 and 4.3.4). Understanding physical mode of sound production will reveal design constraints, which in turn provides a rigorous context for studies on the behavioral, ecological, or evolutionary relevance of acoustic communication. Sonations offer opportunities to examine certain types of questions with simpler experimental methods than are available for vocalizations. The physical mechanisms of sound production can be easy to manipulate experimentally on wild animals (e.g. bird feathers) and do not require surgery. Therefore, large sample sizes and subtle manipulations are available. Natural individual variation is present in sonations just as it is in vocalizations (Garcia et al. 2012a), and in some instances this variation can be extensive, such as when sound-producing feathers are damaged or have a species-atypical shape (Miskelly 2005; Clark 2011; Clark et al. 2013c). As the sound production mechanism is external, it may be easy to quantify how natural morphological differences in the production mechanism (e.g., caused by size, age, sex, wear, or other aspects of condition, such as parasite damage) contribute to variation in the signal, research that is far harder to do noninvasively on vocal morphology.

Another avenue of future research is the relationship between sound and display performance, because many sonations are produced during displays (in birds). There is a direct intrinsic link between sonation form and locomotor performance. Although this intrinsic link constrains acoustic form and makes sonations nonversatile, unlike vocalizations, it also means that sonations have the potential to be intrinsic index signals of locomotor capacity. This is particularly likely because acoustic sensory systems are intrinsically better tuned to measure display attributes such as frequencies, than are visual systems. Therefore, it appears that examining how females use sonations to assess male locomotor performance (Byers et al. 2010) is wide open to future study. That said, the “honesty” of courtship signals remains a debated topic (Prum 2010), and the idea that sonations are indicators of locomotor performance is an adaptive hypothesis to be tested, not assumed.

Finally, the phylogenetic diversity of sonations implies they have evolved hundreds of times independently. This phylogenetic diversity provides a large sample size of independent origins for analyses that explore how communication systems initially evolve, and then diversify. By contrast, vocalization, despite their preeminent place in acoustic biology of vertebrates, have evolved so few times independently that their early origins and context may never be understood fully. As ever-larger phylogenies become available, evolutionary hypotheses can be tested more robustly. The repeated origins of sonations out of adventitious sounds offer the opportunity to examine why and how acoustic communication evolves.

References

- Alben, S., & Shelley, M. J. (2008). Flapping states of a flag in an invicid fluid: Bistability and the transition to chaos. *Physical Review Letters*, *100*, 074301.
- Aldrich, E. C. (1939). *Natural history of the Allen hummingbird (Selasphorus alleni)*. MA thesis, University of California, Berkeley, CA.
- Archibald, H. L. (1974). Directional differences in the sound intensity of Ruffed Grouse drumming. *Auk*, *91*, 517–521.
- Au, W. W. L., & Suthers, R. A. (2014). Production of biosonar signals: Structure and form. *Springer Handbook of Auditory Research*, *51*, 61–105.
- Bae, Y., & Moon, Y. J. (2008). Aerodynamic sound generation of flapping wing. *Journal of the Acoustical Society of America*, *124*, 72–81.
- Baptista, L. F. (2001). The song and dance of hummingbirds. *California Wild*, *54*, 14–20.
- Baptista, L. F., & Matsui, M. (1979). The source of the dive-noise of the Anna's hummingbird. *Condor*, *81*, 87–89.
- Barlow, C. (1967). Ethological units of behavior. In D. Ingle (Ed.), *The central nervous system and fish behavior* (pp. 217–232). Chicago: University of Chicago Press.
- Barrera, J. P., Chong, L., Judy, K. N., & Blumstein, D. T. (2011). Reliability of public information: Predators provide more information about risk than conspecifics. *Animal Behaviour*, *81*, 779–787.
- Barske, J., Fusani, L., Wikelski, M., Feng, N. Y., Santos, M., & Schlinger, B. A. (2014). Energetics of the acrobatic courtship in male golden-collared manakins (*Manacus vitellinus*). *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132482. doi:10.1098/rspb.2013.2482.
- BBC. (2011). Bizarre mammals filmed calling using their quills. Retrieved June 27, 2014, from http://news.bbc.co.uk/earth/hi/earth_news/newsid_9392000/9392070.stm.
- Bennet-Clark, H. C. (1999). Resonators in insect sound production: How insects produce loud pure-tone songs. *Journal of Experimental Biology*, *202*, 3347–3357.
- Bhatt, M., & Bardolia, H. (2006). *Call of Indian birds*, Vol. 1 (CD). Nature Club Surat.
- Blake, W. K. (1986). *Mechanics of flow-induced sound and vibration* (Vol. 1). Orlando, FL: Academic.
- Bostwick, K. S. (2006). Mechanisms of feather sonation in Aves: Unanticipated levels of diversity. *Acta Zoologica Sinica*, *52S*, 68–71.
- Bostwick, K., Elias, D. O., Mason, A. C., & Montealegre-Z, F. (2009). Resonating feathers produce courtship song. *Proceedings of the Royal Society B: Biological Sciences*, *227*, 835–841.
- Bostwick, K. S., & Prum, R. O. (2003). High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). *Journal of Experimental Biology*, *206*, 3693–3706.
- Bostwick, K. S., & Prum, R. O. (2005). Courting bird sings with stridulating wing feathers. *Science*, *309*, 736.
- Bostwick, K., Riccio, M. L., & Humphries, J. M. (2012). Massive, solidified bone in the wing of a volant courting bird. *Biology Letters*, *8*, 760–763.
- Bostwick, K., & Zyskowski, K. (2001). Mechanical sounds and sexual dimorphism in the crested doradito. *Condor*, *103*, 861–865.
- Bro-Jørgensen, J., & Dabelsteen, T. (2008). Knee-clicks and visual traits indicate fighting ability in eland antelopes, multiple messages and back-up signals. *BMC Biology*, *6*, 47.
- Byers, J., Hebets, E. A., & Podos, J. (2010). Female mate choice based upon male motor performance. *Animal Behaviour*, *79*, 771–778.
- Clark, C. J. (2008). Fluttering wing feathers produce the flight sounds of male streamertail hummingbirds. *Biology Letters*, *4*, 341–344.
- Clark, C. J. (2009). Courtship dives of Anna's hummingbird offer insights into flight performance limits. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 3047–3052.
- Clark, C. J. (2011). Wing, tail, and vocal contributions to the complex signals of a courting Calliope hummingbird. *Current Zoology*, *57*, 187–196.

- Clark, C. J. (2012). The role of power versus energy in courtship: What is the ‘energetic cost’ of a courtship display? *Animal Behaviour*, *84*, 269–277.
- Clark, C. J. (2014). Harmonic hopping, and both punctuated and gradual evolution of acoustic characters in *Selasphorus* hummingbird tail feathers. *Plos One*, *9*, e93829.
- Clark, C. J., Elias, D. O., Girard, M. B., & Prum, R. O. (2013a). Structural resonance and mode of flutter of hummingbird tail feathers. *Journal of Experimental Biology*, *216*, 3404–3413.
- Clark, C. J., Elias, D. O., & Prum, R. O. (2011). Aeroelastic flutter produces hummingbird feather songs. *Science*, *333*, 1430–1433.
- Clark, C. J., Elias, D. O., & Prum, R. O. (2013b). Hummingbird feather sounds are produced by aeroelastic flutter, not vortex-induced vibration. *Journal of Experimental Biology*, *216*, 3395–3403.
- Clark, C. J., & Feo, T. J. (2008). The Anna’s hummingbird chirps with its tail: A new mechanism of sonation in birds. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*, 955–962.
- Clark, C. J., & Feo, T. J. (2010). Why do *Calypte* hummingbirds “sing” with both their tail and their syrinx? An apparent example of sexual sensory bias. *American Naturalist*, *175*(1), 27–37.
- Clark, C. J., Feo, T. J., & Bryan, K. B. (2012). Courtship displays and sonations of a male broad-tailed × black-chinned hummingbird hybrid. *Condor*, *114*, 329–340.
- Clark, C. J., Feo, T. J., & van Dongen, W. (2013c). Sounds and courtship displays of the Peruvian sheartail, Chilean woodstar, oasis hummingbird, and a hybrid male Peruvian sheartail × Chilean woodstar. *Condor*, *115*, 560–577.
- Clark, C. J., & Mitchell, D. E. (2013). Allen’s hummingbird (*Selasphorus sasin*). *Birds of North America Online*. <http://bna.birds.cornell.edu/bna/species/501/articles/introduction>
- Darwin, C. (1871). *The descent of man, and selection in relation to sex*. Princeton, NJ: Princeton University Press.
- Delacour, J., & Amadon, D. (1973). *Curassows and related birds* (2nd ed.). New York: The American Museum of Natural History.
- Endo, H., Koyabu, D., Kimura, J., Rakotondraparany, F., Matsui, A., Yonezawa, T., et al. (2010). A quill vibrating mechanism for a sounding apparatus in the streaked tenrec (*Hemicentetes semispinosus*). *Zoological Science*, *27*(5), 427–432.
- Ewing, A. W. (1989). *Arthropod bioacoustics neurobiology and behaviour*. Ithaca, NY: Cornell University Press.
- Feo, T. J., & Clark, C. J. (2010). The displays and sonations of the black-chinned hummingbird (Trochilidae: *Archilochus alexandri*). *Auk*, *127*, 787–796.
- Fletcher, N. H. (1992). *Acoustic systems in biology*. New York: Oxford University Press.
- Fletcher, N. (2013). Shock waves and the sound of hand-clap—a simple model. *Acoustics Australia*, *41*, 165–168.
- Fletcher, N. H., & Rossing, T. D. (1998). *The physics of musical instruments*. New York: Springer.
- Fournier, J. P., Dawson, J. W., Mikhail, A., & Yack, J. E. (2013). If a bird flies in the forest, does an insect hear it? *Biology Letters*, *9*, 20130319. doi:10.1098/rsbl.2013.0319.
- Friedmann, H. (1955). The honey-guides. *United States National Museum Bulletin*, *208*, 1–292.
- Garcia, M., Charrier, I., Rendall, D., & Iwaniuk, A. N. (2012a). Temporal and spectral analyses reveal individual variation in a non-vocal acoustic display: The drumming display of the ruffed grouse (*Bonasa umbellus*, L.). *Ethology*, *118*, 292–301.
- Garcia, M., Charrier, I., & Iwaniuk, A. N. (2012b). Directionality of the drumming display of the ruffed grouse. *Condor*, *114*, 500–506.
- Geyer, T., Sarradj, E., & Fritzsche, C. (2013). Silent owl flight: Comparative acoustic wind tunnel measurements on prepared wings. *Acta Acustica United with Acustica*, *99*, 139–153.
- Hingee, M., & Magrath, R. D. (2009). Flights of fear: A mechanical wing whistle sounds the alarm in a flocking bird. *Proceedings of the Royal Society B: Biological Sciences*, *276*, 4173–4179.
- Hunter, T. A. (2008). On the role of wing sounds in hummingbird communication. *Auk*, *125*, 532–541.
- Hunter, T. A., & Picman, J. (2005). Characteristics of the wing sounds of four hummingbird species that breed in Canada. *Condor*, *107*, 570–582.

- Kingston, T., & Rossiter, S. J. (2004). Harmonic-hopping in Wallace's bats. *Nature*, *429*, 654–657.
- Koch, R. E., Krakauer, A. H., & Patricelli, G. L. (2015). Investigating female mate choice for mechanical sounds in the male greater sage-grouse. *Auk: Ornithological Advances*, *132*, 349–358.
- Konishi, M. (1973). How the owl tracks its prey. *American Scientist*, *61*, 414–424.
- Kroeger, R. A., Gruschka, H. D., Helvey, T. C., et al. (1972). Low speed aerodynamics for ultra-quiet flight (pp. 1–155). Air Force Flight Dynamics Lab, Wright-Patterson Air Force Base, OH.
- Lane, D. F., Servat, G. P., Valqui, H. T., & Lambert, F. R. (2007). A distinctive new species of tyrant flycatcher (Passeriformes: tyrannidae: *Cnipodectes*) from southeastern Peru. *Auk*, *124*, 762–772.
- Lentink, D., Haselsteiner, A. F., & Ingersoll, R. (2015). *In vivo* recording of aerodynamic force with an aerodynamic force platform: From drones to birds. *Journal of the Royal Society Interface*, *12*, 20141283.
- Lighthill, M. J. (1952). On sounds generated aerodynamically. I. General theory. *Proceedings of the Royal Society of London A: Mathematical and Physical Sciences*, *211*, 564–587.
- Manson-Bahr, P. H., & Pye, J. D. (1985). Mechanical sounds. In B. Campbell & E. Lack (Eds.), *A dictionary of birds*. Vermillion, SD: Buteo Books.
- Miller, S. J., & Inouye, D. W. (1983). Roles of the wing whistle in the territorial behavior of male broad-tailed hummingbirds (*Selasphorus platycercus*). *Animal Behaviour*, *31*, 689–700.
- Miskelly, C. M. (1990). Aerial displaying and flying ability of Chatham Island snipe *Coenocorypha pusilla* and New Zealand snipe *C. aucklandica*. *Emu*, *90*, 28–32.
- Miskelly, C. M. (2005). Evidence for 'hakawai' aerial displaying by Snares Island snipe (*Coenocorypha aucklandica huegeli*). *Notornis*, *52*, 163–165.
- Mitchell, D. E. (2000). Allen's hummingbird. In *The birds of North America*, No. 501. Vermillion, SD: Buteo Books.
- Myhrvold, N. P., & Currie, P. J. (1997). Supersonic sauropods? Tail dynamics in the diplodocids. *Paleobiology*, *23*, 393–409.
- Nelson, S. K., & Hamer, T. E. (1995). Nesting biology and behavior of the marbled murrelet. In C. J. Ralph (Ed.), *Ecology and conservation of the marbled murrelet* (pp. 57–68). Berkeley, CA: Pacific Southwest Research Station, USDA.
- Norberg, R. Å. (1991). The flappet lark *Mirafra rufocinnamomea* doubles its wingbeat rate to 24 hz in wing-clap flight display: A sexually selected feat. *Journal of Experimental Biology*, *159*, 515–523.
- Ortiz-Crespo, F. I. (1980). *Agonistic and foraging behavior of hummingbirds co-occurring in central coastal California*. PhD thesis, University of California, Berkeley.
- Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature*, *409*, 185–188.
- Podos, J., Southall, J. A., & Rossi-Santos, M. R. (2004). Vocal mechanics in Darwin's finches: Correlation of beak gape and song frequency. *Journal of Experimental Biology*, *207*, 607–619.
- Prum, R. O. (1993). Phylogeny, biogeography, and evolution of the broadbills (Eurylaimidae) and asiatics (Philepittidae) based on morphology. *Auk*, *110*, 304–324.
- Prum, R. O. (1998). Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae). *Animal Behaviour*, *55*, 977–994.
- Prum, R. O. (2010). The Lande-Kirkpatrick mechanism is the null model of evolution by intersexual selection: Implications for meaning, honesty, and design in intersexual signals. *Evolution*, *64*, 3085–3100.
- Pytte, C. L., & Ficken, M. S. (1994). Aerial display sounds of the black-chinned hummingbird. *Condor*, *96*, 1088–1091.
- Randall, J. A. (2001). Evolution and function of drumming as communication in mammals. *American Zoologist*, *41*, 1143–1156.

- Reddig, V. E. (1978). Der ausdrucksflug der Bekassine (*Capella gallinago gallinago*). *Journal für Ornithologie*, 119, 357–387.
- Richardson, M. H. (1997). Is it a mode shape, or an operating deflection shape? *Sound and Vibration Magazine*, 31(1), 54–61.
- Riede, T., Suthers, R. A., Fletcher, N. H., & Blevins, W. E. (2006). Songbirds tune their vocal tract to the fundamental frequency of their song. *Proceedings of the National Academy of Sciences of the U S A*, 103(14), 5543–5548.
- Robillard, T., Montealegre-Z, F., desutter-Grandcolas, L., Grandcolas, P., & Robert, D. (2013). Mechanisms of high-frequency song generation in brachypterous crickets and the role of ghost frequencies. *Journal of Experimental Biology*, 216, 2001–2011.
- Rodgers, T. L. (1940). The dive note of the Anna hummingbird. *Condor*, 42, 86.
- Rusch, D. H., Destefano, M. C. R., & Lauten, D. (Eds.). (2000). *Ruffed grouse (Bonasa umbellus)* (Vol. 515). Ithaca, NY: Cornell Laboratory of Ornithology.
- Sarradj, E., Fritzsche, C., & Geyer, T. (2011). Silent owl flight: Bird flyover noise measurements. *AIAA Journal*, 49, 769–779.
- Schultz, J. S., Hertel, F., Bauch, M., & Schlinger, B. A. (2001). Adaptations for rapid and forceful contraction in wing muscles of the male golden-collared manakin: Sex and species comparisons. *Journal of Comparative Physiology A*, 187, 677–684.
- Stark, R. D., Dodenhoff, D. J., & Johnson, E. V. (1998). A quantitative analysis of woodpecker drumming. *Condor*, 100(2), 350–356.
- Sueur, J., Tuck, E. J., & Robert, D. (2005). Sound radiation around a flying fly. *Journal of the Acoustical Society of America*, 118, 530–538.
- Trail, P. W., & Donahue, P. (1991). Notes on the behavior and evology of the red-cotingas (Cotingidae: *Phoenicircus*). *Wilson Bulletin*, 103, 539–551.
- Tuck, L. (1972). *The snipes: A study of the genus Capella*. Ottawa, Canada: Canadian Wildlife Service.
- Unsworth, A., Dowson, D., & Wright, V. (1971). ‘Cracking joints’: A bioengineering study of cavitation in the metacarpophalangeal joint. *Annals of the Rheumatic Diseases*, 30, 348–358.
- Vogel, S. (1994). *Life in moving fluids*. Princeton, NJ: Princeton University Press.
- Wilson, B., Batty, R. S., & Dill, L. M. (2003). Pacific and Atlantic herring produce burst pulse sounds. *Proceedings of the Royal Society B: Biological Sciences*, 271, S95–S97.
- Wilson, T. A., Beavers, G. S., DeCoster, M. A., Holger, D. K., & Regenfuss, M. D. (1971). Experiments on the fluid mechanics of whistling. *Journal of the Acoustical Society of America*, 50, 366–372.
- Zeigler, H. P., & Marler, P. (2012). *Neuroscience of birdsong*. Cambridge, England: Cambridge University Press.