

Commentary

Signal or cue? Locomotion-induced sounds and the evolution of communication

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The thrumming motor of an approaching car is salient to a pedestrian or cyclist. The source is usually an internal combustion engine, which intrinsically makes a fair amount of noise during operation. At low speeds, this internal combustion is the primary source of automobile noise. Despite its relevance, this noise is clearly a cue and not a signal, because the sound is an incidental by-product of the motor. After all, internal combustion cars have a muffler to reduce motor noise. A few years ago, electric automobiles arrived on the market, which have intrinsically quieter electric motors. Their relative stealth has posed a new risk to pedestrians and cyclists, who could not hear these new cars as well. As a result, the U.S. National Highway Traffic Safety Administration requires that, starting in 2019, electric cars must produce extra sound when they drive at low speeds (NHTSA, 2016). The addition of a noise-maker that produces extra sound during motion is clearly a signal to pedestrians. This sound, initially just a cue of an internal combustion engine, has been converted into an intentionally produced signal in electric cars. A new communication signal has 'evolved'.

This automotive example has many similarities to the sounds animals make as they move, which I call 'locomotion-induced sounds'. The study of locomotion-induced sounds and the role of these sounds in communication is not well advanced. Here, I

explore a topic that was not entirely resolved in my recent review (Clark, 2016). Specifically, I explore the criteria used to decide whether a poorly studied locomotion-induced sound is a signal or a cue.

There are two models of how signals arise. The ritualization (Huxley, 1923; Tinbergen, 1952), or 'sender precursor' (Bradbury & Vehrencamp, 2011), model of how signals initially arise out of cues over evolutionary time is the model we apply below. The other model of signal evolution is the perceptual bias model, in which receiver responses arise prior to sender traits (Ryan & Cummings, 2013). The arguments below are couched in the context of ritualization, because cues are central to the arguments presented below, but it is unclear whether the concept of a cue has any utility in the perceptual bias model.

The 'evolution' of electric car noises reflects the stages of ritualization, which are as follows. (1) Exaptation (Gould & Vrba, 1982): a motion evolves that generates adventitious sound as a by-product. For example, the noisy internal combustion engine is invented and cars with internal combustion engines begin to replace horse-based transport. (2) Receivers respond to the cue, raising the possibility of selection exerted on the sender. For example, once internal combustion engines are familiar, pedestrians use this sound to detect an approaching car. (3) Ritualization: mechanisms that produce the sound respond to selection on the sender, the sound becomes evolutionarily modified, thereby becoming a signal (Darwin, 1871; Maynard Smith & Harper, 2003; Prum, 1998). For example, electric cars, as they are not intrinsically

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noisy, acquire noisemakers. Extant animals and the sounds they make as they move may fall anywhere within these three stages (e.g. Scott et al., 2010).

Not all sounds produced by animals as they move are already ritualized. The world is full of noises that are cues. As you sit and read this, perhaps the fan on your computer whirrs, or the toenails of a dog or cat click on the floor as it walks by. Within a medium (air, water, soil), all motions make sound, and all sounds arise from motion (Clark, 2016). Sometimes this axiom is trivial, because many motions are functionally silent. For example, heartbeats generate sound that is inaudible (except with a stethoscope). But the broader point holds: sounds arising from animal motion are ubiquitous. Hereafter I call these locomotion-induced sounds; this term is neutral to function. Locomotion-induced sounds cannot all be signals, although they have evolved into signals many times in animals including various birds (Clark & Prum, 2015; Clark, 2016), the footdrumming of rodents (e.g. kangaroo rats, *Dipodomys* spp.) and other mammals (Randall, 2001, 2013), or wing clicks used for echolocation in certain bats (Boonman, Bumrungsri, & Yovel, 2014). Motion-induced sounds are present in many insects, such as the wing hum of midges and mosquitoes (Cator, Arthur, Harrington, & Hoy, 2009; de Silva, Nutter, & Bernal, 2015), or crepitation of grasshoppers (Otte, 1970). Some of the recent surge in interest in 'nonvocal' sounds of birds was inspired by Bostwick and Prum (2003), who used the term 'sonations' to mean nonvocal sounds that serve as signals. Sounds that are not sonations are 'adventitious sounds', or cues that are simply a by-product of locomotion, such as ordinary human footsteps.

Researchers studying putative vertebrate sonations, particularly of birds, often have a background in the study of vocalizations. Studies of sonations thus get coloured by implicit assumptions borrowed from the study of vocalizations. (Vocabulary too: what does 'nonvocal' actually mean? Can the vocal tract really produce nonvocal sound?). Vocalizations are noises produced by the respiratory and digestive tract, parts of which (e.g. larynx, syrinx) are specialized for the production of sound. Vocal adventitious sounds, such as coughs, wheezes or burps, seem to be relatively rare. Therefore, acoustic emissions of the vocal tract are often reasonably assumed to be signals, even if their function is unknown. But this is neither a safe nor a conservative assumption in the study of locomotion-induced sounds.

The rigorous approach to establishing that a sound is a sonation is to apply the same standard that applies to any other putative signal. One definition of a signal entails three criteria: a signal, on average, conveys information that both (1) increases the fitness of the sender (2) and the receiver, and (3) has evolved to do so (Bradbury & Vehrencamp, 2011; Maynard Smith & Harper, 2003; Scott-Phillips, 2008). Anything else is a cue: it has not evolved for the purpose of conveying information. It is not sufficient for a putative signal to contain information useful to both sender and receiver, as cues can do this as well (Maynard Smith & Harper, 2003; Scott-Phillips, 2008) – saliency arises in stage 2 of the evolution of sonations. Recognizing and responding to the sound of the internal combustion of an automobile might increase the fitness of a pedestrian, and perhaps also of the driver, but it is not a signal until it becomes evolved for that purpose, as in noisemakers on electric cars. According to these three criteria, an animal signal can be identified through experiments that demonstrate a benefit to sender, a benefit to receiver, and that it has evolved. Demonstrating all three of these criteria has been done for relatively few signals, and even fewer sonations (e.g. Murray, Zeil, & Magrath, 2017).

Evidence arising out of experimental manipulations designed to test the above criteria will always be the most rigorous approach to diagnose signals from cues. As the necessary work to do such manipulations is time consuming, most examples of possible

sonations have not been studied in this way. It is these poorly studied examples that are the focus here. When there is limited information, for example, when males of a newly discovered species of tyrant flycatcher are observed making a noteworthy sound in a flight display, and found to have distinctively twisted wing feathers (Lane, Servat, Valqui, & Lambert, 2007), what are the criteria by which we decide this sound is a likely signal?

To answer this question, I outline below five theoretical properties of locomotion-induced sounds that have practical bearing on their diagnosis, building on ideas and terminology presented in Clark (2016). While these five properties are not unique to locomotion-induced sounds, they are useful to enumerate, since the contours of the problem differ from those for vocalizations. For example, a property may be hard to assess in vocalizations because invasive techniques (e.g. surgery) are needed, but it can be easy to ascertain by eye/ear for locomotion-induced sounds (see Property 1, below). Other properties can be trivial to assess with vocalizations, but are not trivial with locomotion-induced sounds (see Properties 3, 4 and 5 below). I convert these theoretical properties into a practical set of criteria for assessing whether a given sound is a signal, along with a heuristic set of seven questions to guide assessment of empirical examples (presented in Supplementary Table S1). I then apply these criteria to some recently studied examples of locomotion-induced sounds that authors have stated are sonations. The arguments and examples presented here are mostly couched in the context of flying animals, especially birds, as birds have been a recent focus of research. The term 'locomotion' used here follows the extremely broad definition of Barlow (1968, p. 228): 'Thus in the end [all of behaviour] is locomotion, respiration, or feeding'. The arguments presented here are intended to be valid for most sound produced by motion of an animal's integument, including gestures, although certain integumentary structures (e.g. air sacs, buccal cavity, human lips) contribute to production of sounds best regarded as vocal.

FIVE PROPERTIES OF LOCOMOTION-INDUCED SOUNDS

Property 1

Locomotion-induced sounds have a kinematic basis. This property is an axiom underlying the study of locomotion-induced sound (Clark, 2016). Sound does not arise *de novo*, it arises out of relative motion within a fluid medium such as air or water. While the source motions that produce vocalizations arise hidden inside the animal (in the larynx or syrinx), and so are not readily observed, locomotion-induced sounds are produced by observable external motions of the animal. This means that there is a '1 to 1' match between a component of the animal's kinematics (motions) and the ensuing sound (Clark, 2009). If an experimenter has correctly identified the mechanism, and thus knows the source of sound (Clark, 2016), then a regression of timing of motion against timing of a sound element, in theory, has a slope of 1.0 and an r^2 of 1.0, after accounting for measurement error. The motions and sounds are simply two manifestations of the same phenomena. This also means that one can use either modality, motion or sound, to analyse sonations. Video or sound recordings of a sonation provide complementary lines of evidence of the same underlying phenomena.

Property 2

The mechanism that produces a sound can be specific, subtle or hidden, and thus hard to identify. The 1:1 match can be difficult to discern from other kinematic events that are correlated with the mechanism. Consider the example of a person that takes five steps.

During the five steps, suppose four distinct -tic- sounds are produced: -tic- -tic- ——— -tic- -tic-. The four -tic- sounds align with the first, second, fourth and fifth steps, but the third is missing. This missing sound implies that 'takes a step' is not the source of sound per se, since there are five steps but four sounds. Rather, a reasonable hypothesis is that the substrate for the third step was different (e.g. the third step was on carpet rather than linoleum). Under this hypothesis, the 1:1 match with the sound is a specific kinematic: 'step on linoleum'. Alternately, perhaps a pebble has become lodged in the tread of the person's shoe, such that the -tic- sound is produced only when the person's shoe strikes the ground in a certain orientation. That is to say, the key element could be 'steps a certain way', in which the sound depends on the precise kinematics of the foot, plus the pebble, as the foot strikes the ground.

A similar hypothetical example: a dove flaps its wings five times and produces a tonal sound in four out of those five flaps. For flutter-induced sound (of certain feathers), tonal sound is only produced when several conditions are met. One such condition is that the local air velocity exceeds a threshold, U^* (Clark, Elias, & Prum, 2011). The motion that produces the sound is thus not as general as 'flaps wing', but one hypothesis is 'flaps wing fast enough to exceed U^* ', which could have been exceeded in four out of five wing beats.

The difficulty with diagnosing many sonations comes from an interaction of the properties described here. If the sound is produced only in certain contexts (see Property 4 below), it could be involuntary. Alternately, it could be under voluntary control of a 'hidden switch'. The switch is 'hidden' from the investigator because it is a subtle, hard to identify component within the kinematics of locomotion (Clark, 2016). This uncertainty about the mechanism means that it can be difficult to tell whether certain sounds are voluntary.

Property 3

Locomotion-induced sounds vary in voluntariness. I specify two types of voluntariness, the first of which is sound voluntariness. Sound voluntariness is the degree to which an animal can modulate sound production while it is moving, independent of the other general kinematics of locomotion. Many sounds are mostly or entirely voluntary, such as human hand clapping or manakin wing snaps. At the other end of the spectrum, entirely involuntary sounds are those that simply cannot be avoided. For instance, a bell on a horse may jingle involuntarily with every step the horse takes (as a signal), or snow or dry leaves may crunch underfoot involuntarily (as a cue). Similarly, the wing hum of flying insects and hummingbirds is involuntary, because these sounds are simply a physical manifestation of Newton's third law of an equal, opposite reaction to the aerodynamic forces produced as an animal flaps its wings. Although the term voluntary connotes 'free will' when applied to people, consciousness is not a necessary component of the word 'voluntary' as used here; the animal need not be aware of what it is doing.

In between entirely voluntary and entirely involuntary are sounds that are somewhat voluntary, such as human footsteps. One can change shoes, or change footstep kinematics, stomping or tiptoeing to modify the sound of feet striking the ground, while still walking. But the only way to entirely eliminate making footstep sounds is to not walk: locomotion itself is also voluntary.

Locomotion voluntariness is the other type of voluntariness. A mouse that freezes in the presence of an owl, ceasing locomotion, thus does not make locomotion-induced sound that would reveal its position. While locomotion voluntariness is important when considering trade-offs in animal decision making, locomotion

voluntariness is best considered a part of Property 1. Since Property 1 states that sound is a by-product of locomotion, it follows that ceasing locomotion ceases sound production. The difference between locomotion voluntariness and sound voluntariness is specifically about whether production of the sound per se can be modulated while locomotion or other underlying kinematics are still taking place. Sound voluntariness is the ability to modulate the sound of footsteps while still walking. Hereafter, references to voluntariness refer specifically to sound voluntariness, and references to involuntary sounds could be read as locomotor voluntariness if the reader prefers. Figure 1 provides some examples of sounds that vary in their voluntariness.

This argument only skims the surface of what is clearly a complicated topic. Having just made a distinction between voluntary and involuntary sounds, there is a caveat: context matters. A sound that is voluntary in one context can be involuntary in another. For instance, male black-chinned hummingbirds, *Archilochus alexandri*, during a display dive spread their tail to make loud tail sounds (Feo & Clark, 2010) and within the kinematics of diving, this motion of spreading the tail seems entirely voluntarily. Yet during a chase, males sometimes make the same sound as they spread their tails to manoeuvre (C. J. Clark, personal observation). Within the context of fleeing from another male, spreading the tail may be involuntary as it is a necessary part of a manoeuvre to escape (or pursue) a rival. Basically, having an 'instrument' that is voluntarily played at one time might result in its involuntarily producing sound at others. Humans routinely experience this. A Morris dancer that straps bells to her leg, then shakes her leg to intentionally produce a certain tempo of jingling in a dance also produces involuntary jingling sound as she walks to and from the dance area. This question of whether a sound is produced voluntarily is central to determining whether the sound is produced with 'modified behaviour', per Property 5, below.

Property 4

Locomotion-induced sounds vary in their context specificity. Specificity lies on a continuum; at one end are sounds produced only during a single kinematic context, such as only during a display, or some other infrequent condition (such as when moving fast). At the other end of the spectrum are sounds produced during all locomotion, such as during all walking (the sound of horses' hooves on ground) or flight (the wing hum of a hummingbird's or a mosquito's wings).

Specificity must not be confused with voluntariness (Fig. 1). There is overlap between the two: any sound that is voluntary will be modulated by the animal, e.g. produced at some times but not others, and thus must have some context specificity (e.g. upper right of Fig. 1). And if an animal produces a sound continuously during locomotion (i.e. it has little or no context specificity), then it must also be involuntary as it has little scope to be produced voluntarily (lower left of Fig. 1). However, sounds that are entirely involuntary may also be context specific (upper left of Fig. 1). Specificity depends on the mechanism by which the sound is produced. If the mechanism that produces sound has conditions that are rarely met, for example the sound is only produced when the animal moves at high speed, that sound may be highly context specific and yet still involuntary.

Property 5

To be a signal, either morphology or behaviour, or both are modified to produce the sound. A cue becomes a signal when it is ritualized: it acquires, either through evolution or learning, a morphological or behavioural phenotypic character specifically for

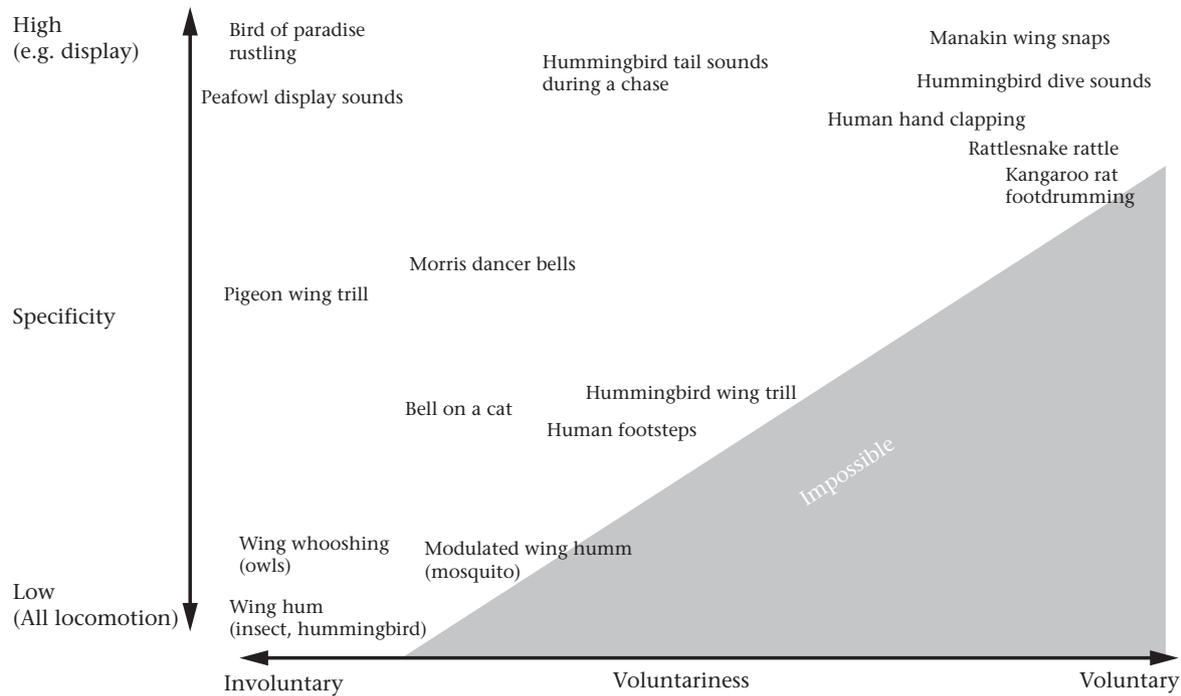


Figure 1. Voluntariness versus specificity of locomotion-induced sounds. Voluntariness is the degree to which the animal can modulate a locomotion-induced sound while undergoing ordinary locomotion. Specificity is the degree to which the sound is present in all versus only specific types of locomotion. Placement of individual examples is not intended to be taken too literally, as it will also be influenced by other unspecified conditions (is the Morris dancer allowed to take her bells off?).

the acoustic qualities of the sound it produces. If the sound is produced by neither modified morphology nor modified behaviour, it cannot have evolved for communication, and is best regarded a cue.

Modified morphology as a signal can be self-explanatory: the animal itself has an 'instrument' with a functional morphology tied to sound production (Clark, 2016), even if production of the sound is involuntary. But the converse is not true: there is no need to assume that for a special communication sound to be produced, there must be modified morphology. For example: human hands do not have any morphological adaptations to produce clapping, finger snapping or knocking on a door, yet these are three indisputable human communication sounds. Clapping, finger snapping or knocking are all the product of voluntary, modified behaviour to produce distinctive sounds used in human communication. It is sufficient to modify behaviour to produce a signal (Lotem, Wagner, & Balshine-Earn, 1999); modified morphology is not essential.

In modified behaviour, the animal's kinematics depart from the apparent normal kinematics underlying the behaviour. For example, a golden-collared manakin, *Manacus vitellinus*, suddenly snaps its wings together during a manoeuvre, when wing–wing collisions are not a part of similar wing beats in ordinary flight (Bodony et al., 2016; Bostwick & Prum, 2003). Modified behaviours are evaluated against the animal's regular kinematics, the ordinary kinematics of the underlying behaviour. This can be tricky to assess. Visual observation of a display may be sufficient to reveal modified behaviour, while in other cases modified behaviour can only be assessed with a high-speed video (Bostwick & Prum, 2003; Clark & Feo, 2008). Even high-speed videos by themselves may be frustratingly inconclusive. This occurred to me when studying *Smithornis* broadbills (Clark, Kirschel, Hadjioannou, & Prum, 2016). The high-speed videos of displaying *Smithornis* broadbills, when they are producing a loud sound with the wings, look like the kinematics of ordinary bird wing flaps, when no distinctive sound is present. There was nothing clearly modified about the motion of each or any

individual wing beat (Clark et al., 2016). Modified behaviours are easiest to diagnose if they are temporally discrete events within a longer sequence of ordinary kinematics, such as if one wing beat is different from the others. If every wing beat or footfall in a long sequence is similar, it requires careful justification to call any or all of them modified, such as in the mosquito and midge wing sounds described below.

CRITERIA FOR SONATIONS

The previous section provided abstract, theoretical properties of locomotion-induced sounds. I developed a heuristic guideline to assist in assessment of empirical examples for which only limited information is available (see [Supplementary Table S1](#)). There are, in practice, four types of evidence that authors have used to infer that a sound is a sonation. In order of easiness and robustness of diagnosis, they are 'modified morphology', 'undirected display', 'modified behaviour' and 'acoustic quality'. I applied [Table S1](#) to Clark and Prum's (2015) list of putative sonations produced by the wings or tail of birds, the results of which are presented in [Supplementary Table S2](#). I then applied the heuristic questions in [Table S1](#) to some other literature examples, including examples from outside of birds (see below). Next I discuss these four criteria, with comments on patterns in Clark and Prum's (2015) list of putative sonations.

Modified Morphology

Modified morphology can be the strongest or least ambiguous criterion for sonations. Rattlesnakes have a rattle, or many birds have feathers with highly modified shape, in which the morphological trait has no other known function aside from sound production.

Ambiguous cases are not hard to find. Authors sometimes attribute sonations to modified morphology without presenting the morphology in question. For example, [Calf, Downs, and Cherry](#)

(2003) measured the 'almost triangular bulge on the sixth primary feather' of the Cape sugarbird, *Promerops cafer*. A figure is warranted, even if such morphology might be obvious to an investigator (and the morphology of Cape sugarbird is clearly specialized: Fig. 2). Authors occasionally assert modified morphology is present when the case appears ambiguous. Sick (1965) suggested that primary feathers P8 and P9 of *Conopophaga lineata* are specially formed, but his image (and inspection of a couple of specimens in the Yale Peabody Museum) did not confirm easily identified morphological specialization for sound production in the wings of this species. Similarly, Chapin (1953) stated that broadbills in the genus *Smithornis* have modified outer wing feathers, but Clark et al. (2016) were unable to support this assertion. Upon observing a bird making a sound during a display, these authors may have intuitively used the modified behaviour criterion to identify this sound as a sonation, and assumed that if the animal makes a sonation, morphology must be modified, leading them to overstate the case for modified morphology. This is not to claim that *Conopophaga* or *Smithornis* lack modified morphology. Rather, modification can be subtle and hard to identify with certainty, as described further in a couple of the examples, below.

Undirected Display

An undirected display is simply a special case of modified behaviour, in which the context makes diagnosis particularly easy. A nuanced assessment of voluntariness is unnecessary, as the entire behaviour is voluntary. Undirected sounds are broadcast into the environment to potential receivers that are out of sight, such as the vocal songs of a bird, gecko or frog. Some birds instead produce locomotion-induced sounds in this same way. Provided the animal does not also vocalize during this display, sounds produced in this way are easily diagnosed as a sonation. For example, *Smithornis* broadbills or lesser florican, *Syphoetides indica*, broadcast wing-generated sounds in an undirected fashion into the environment (Table S2). But if the animal also vocalizes, and if the locomotion-induced sounds are quiet, those locomotion-induced sounds might be a by-product of producing the vocalization. For example, vermillion flycatcher, *Pyrocephalus rubinus*, produces a vocal dawn song either from a perch or while in flight. During this dawn song flight they sometimes also produce a distinctive but not especially loud wing sound (Clark & Prum, 2015). Although acoustically distinctive, it is possible that the wing sound is a by-product of flight behaviours that support vocalizing.

Modified Behaviour

If the kinematics are clearly for producing the sound, then the sound is a sonation according to the modified behaviour criterion.

Fifteen examples in Table S2 were diagnosed under a relatively generous reading of modified behaviour. In practice, modified behaviour is often hard to diagnose under two circumstances: when it is challenging to tell whether the sound is under voluntary control ('hidden switch' hypothesis mentioned in Property 2, above); or in multimodal displays in which it is hard to tell whether the behaviour is modified for sound production per se, rather than for another function, such as a visual modality. I further discuss both of these aspects, below.

Acoustic Quality

It is reasonable to hypothesize that a sound that strikes a human as noteworthy could be evolved specifically as a signal. For example, is the sound loud, or tonal, or produced in a time-varying way, suggesting a physical acoustic mechanism that is unlikely to evolve solely as a by-product? Does it fall within the sensitive range of a receiver's ears? Do other species, such as close relatives, not produce the same sound in the same context? Putative sonations were identified by this criterion because they lacked data clearly in support one of the other criteria. Some, based on extant recordings and/or literature descriptions analysed by Clark and Prum (2015), appear to be dubious sonations, including the wing sounds produced by becard (*Pachyramphus* spp.), tityras (*Tityra* spp.) or certain ducks (*Anas* spp.) during display. Others were sounds that are likely sonations but for which no data are available to satisfy one of the stronger criteria, such as the sounds produced by *Heterocercus* manakins (Alonso, 2000) or little curlew, *Numenius minutus* (Labutin, Leonovitch, & Veprintsev, 1982). Acoustic quality is the weakest basis for deciding that a sound might be a sonation. Sounds diagnosed according to this criteria are best regarded as a hypothesis. If the sound in question really is a sonation, then additional research will uncover evidence supporting either the modified morphology or modified behaviour criteria.

SOME LITERATURE EXAMPLES

The following is not an attempt at a review; for example, I have not done justice to arthropod sounds, much of which falls under the purview of locomotion-induced sounds as defined here. Instead, the following examples are illustrative of concepts and challenges in study of locomotion-induced sounds. The first four examples, three of which are phasianids (grouse, peafowl), are about multimodal displays, where courtship displays involve a visual component with associated locomotion-induced sounds. This leads to the question of whether the sounds are signals per se, or are acoustic cues produced during visual displays. The examples that then follow are about modified morphology, three of which are columbids (doves, pigeons), a clade in which no species are yet known to



Figure 2. The 'paddle' of primary 6 of the Cape sugarbird, *Promerops cafer*, present in adult males (left) but not in females (right), is an example of modified morphology linked to sound production. Images courtesy of Alan Lee.

exert any sort of voluntary control over their wing sounds, and thus the question is whether they have modified morphology. The final two examples are nonavian and relate to taxa in which only modified behaviours are known.

Ruffed Grouse

Male ruffed grouse, *Bonasa umbellus*, perch on logs in the forest understory and produce a loud, low-frequency sound with their wings that is audible at long distances (Garcia, Charrier, Rendall, & Iwaniuk, 2012; O'Neil, Charrier, & Iwaniuk, 2018). This sound is clearly a sonation, because it is produced in an undirected display and does not contain loud vocalizations. Unlike most species producing locomotion-induced sounds during an undirected display, there is no documentation of modified morphology, which may be of interest for future work to examine.

Sage Grouse

During multimodal displays for females, male sage grouse, *Centrocercus urophasianus*, produce a frequency-modulated 'swish' sound as the wings are rubbed over stiffened breast feathers (Koch, Krakauer, & Patricelli, 2015; Wiley, 1973). The stiffened breast feathers could be modified for sound production, or they could be a visual ornament. Likewise, the wing motion may be modified behaviour, but the motions could be interpreted as a visual display. As the swish sound is tonal and frequency modulated (Koch et al., 2015), acoustic structure strongly suggests that it is not an incidental by-product of motion, because frictional sounds are usually atonal (Akay, 2002). Thus, evidence that this sound is a sonation arises from the acoustic quality criterion, which implies a physical acoustic mechanism that would arise out of modified morphology. Future work could put the inference of modified morphology on firmer footing by further examining the functional relationship between the stiffened breast feathers and the acoustic structure of the sound.

Peafowl

Male peafowl, *Pavo cristatus*, shake their erect trains (tail covert feathers) for females in what are clearly multimodal displays with a strong visual component (Yorzinski, Patricelli, Babcock, Pearson, & Platt, 2013). The feathers are mechanically tuned such that the colourful eyespots remain relatively stationary while the base of the covert feathers is vibrated by the bird (Dakin, McCrossan, Hare, Montgomerie, & Kane, 2016). No part of the morphology is known to be modified for sound production per se, since the tuning of the feather vibratory properties may be for visual effect. Likewise, there are not clear modified behaviours, since the conservative assumption is that the kinematics are for a visual display.

The shaking produces a broadband sound, apparently caused by the feathers rubbing and colliding (Dakin et al., 2016). The spectrum of this sound extends down into infrasound because they are vibrated at low frequency (Freeman & Hare, 2015). Freeman and Hare (2015) played back parts of the bandwidth of the sound, such as only the infrasound component of display sounds (this bandwidth limitation was necessary due to the difficulty of generating infrasound). They found that target peafowl changed behaviour (although their effect size was small; their Figure 3) in response to playback of these sounds, suggesting that the playback sounds were salient, and therefore concluding that the sound of the display is a signal.

This is a weak basis for claiming that these sounds are sonations. Cues can be salient, per stage 2 of the evolution of sonations. Better evidence would entail demonstrating that an aspect of the

morphology is modified for sound production; demonstrating that the sound has function at distances over which visual signals do not transmit (i.e. showing that the display can be undirected); demonstrating that the kinematics produce acoustic effects above and beyond a visual effect; or have an acoustic quality that suggests it is not simply a by-product of a visual display. In short, I am sceptical whether this sound is a sonation, based on current evidence, because it is difficult to imagine how this display would sound different if it were a by-product of a strictly visual display.

Blue-capped Cordon Bleu

Both sexes of blue-capped cordon bleu, *Uraeginthus cyanocephalus*, produce sounds by rapidly striking a foot against a perch during a directed display that also features song (Ota, Gahr, & Soma, 2015, 2017). No modified morphology is described. Whether this behaviour constitutes modified behaviour is somewhat unclear; the motions could be construed as a multimodal visual display. However, unlike the peafowl example above, the feet also lack clear visual ornamentation, as might be expected if foot motions were predominantly a visual display. The acoustic quality of the sound suggests that this is a sonation, as it has an amplitude similar to vocalizations and louder than other footstep sounds. Accordingly this sound is tentatively identified as a sonation according to the acoustic quality criterion and possibly the modified behaviour criterion (Ota, Gahr, & Soma, 2017). Further support for this hypothesis would entail further testing the modified behaviour criterion, such as by testing whether the foot motions that produce this sound are also a visual display; or determining how the kinematics of foot motion affect sound production.

Crested Pigeon

Like many columbids, both sexes of crested pigeons, *Ocyphaps lophotes*, produce a distinctive wing trill during flight comprising a pair of tones produced with each flap of the wings. Wing feather P8 is distinctly modified, narrowed and stiffened, and produces one of the two sounds when tested in a wind tunnel (Clark & Prum, 2015), suggesting that its form fits the function of producing sound. The trill is produced in all flight (it has low specificity, Fig. 1), although it also intrinsically varies with mode of flight, because (for instance) birds taking off in alarm flap their wings at a higher rate, producing a higher tempo of wing sound. This is not voluntary, as the wings must be flapped faster to take off faster (e.g. with greater acceleration). Playback experiments demonstrate that these sounds are salient to other pigeons (Hingee & Magrath, 2009; Murray et al., 2017). Playback of the sound of a pigeon taking off normally does not elicit an alarm response in receivers, but playback of the sound of a pigeon taking off in alarm (with elevated tempo) does elicit a response. The acoustic structure (i.e. altered tempo) is a by-product of the kinematic context. This is an indisputable sonation, on account of the modified morphology of feather P8. As there is no evidence that this sound is voluntary (Hingee & Magrath, 2009; Murray et al., 2017), the playback experiments demonstrate saliency and reveal function, but it is the modified morphology that establishes that this sound has evolved and is thus a signal.

Zenaida Dove

In the zenaida dove, *Zenaida aurita*, some individuals produce a tonal wing trill in flight, especially in take-off when the wings are flapped hard. Barrera, Chong, Judy, and Blumstein (2011) documented that the sound was more likely to be produced when doves took off at a steep angle ($\geq 45^\circ$) than at a shallow angle. Barrera et al. (2011) suggested that this sound is voluntary, but they

conflated specificity with voluntariness (Fig. 1). The simpler explanation is that the conditions under which this sound is produced are specific. For instance, the tonality of the sound suggests it is produced by flutter, in which local wing velocity must exceed a critical velocity, U^* , in order for sound to be produced. U^* is more likely to be exceeded when a bird flaps its wings hard enough to take off at a steep angle. There is no documentation of modified morphology, or modified behaviours, and the acoustic quality of the sound is weak evidence at best, since flutter so easily produces tonal sounds, especially in birds with high wing loading (Clark & Prum, 2015). There is no clear evidence that this is a sonation. Given that this sound is produced during ordinary flight, one way to show this sound is a sonation is to find evidence that it is produced with modified morphology.

Rock Pigeon

Both sexes of rock pigeon, *Columba livia*, sometimes produce a tonal sound in flight. Niese and Tobalske (2016) documented that the sound is produced by aeroelastic flutter of a region of the inside vane of feather P10, in a region of the feather that has curved barbs (their Figure 1). They indicate that this morphology is specialized for sound production, and that therefore this sound may be a sonation. However, there is a simpler interpretation of this morphology. Curved barbs are common in pennaceous feathers, and changes in barb curvature are simply one way overall feather shape may change (Feo, Simon, & Prum, 2016). This sound could simply be a by-product of selection on feather shape for aerodynamic function. Niese and Tobalske (2016) found that the force coefficient of P10 is lower relative to feathers P9 or P1. But the crucial comparison is not between P10 and P9, which are different shapes and occupy different parts of the wing (hence serving different functions). A better comparison is between P10 of this species and of a close relative that does not make the sound. It remains possible that this morphology and ensuing sound has arisen in response to selection on feather shape for other reasons. The best way to demonstrate that this is a sonation is through additional comparative work showing that the morphology is in fact modified for sound production; or to document modified behaviour. This example shows how modified morphology can be difficult to ascertain with certainty.

Red-billed Streamertail

In the male red-billed streamertail, *Trochilus polytmus*, modified morphology can be subtle, and potentially difficult to isolate or pin down. Adult males produce a distinctive ‘whirring’ sound in ordinary flight as a type of wing trill, generated by primary wing feathers P8 and P9 (Clark, 2008). High-speed videos show that the outer wing feathers bend in flight, producing a gap between P8 and P9, which flutter to produce the ‘whirring’ sound. Females and other species lack this bending and the gap, and do not make the sound, providing indirect evidence that there is subtle, unidentified modified morphology of P8 and P9 that is invisible to the naked eye (Clark, 2008). Most other hummingbird species that produce wing trills also have displays with modified behaviours that accentuate the wing sound. Documentation of displays in which this sound is actively modulated would strengthen the case that this wing sound is a sonation in this species.

Footdrumming in Mammals

Many mammals produce footdrumming or stamp their feet (as reviewed by Randall, 2001, 2013). Of these, the most studied example is footdrumming produced by both sexes of kangaroo rats

(*Dipodomys* spp.). These thumping sounds are produced by their hindfeet impacting the substrate, and vary temporally by individual and in different behavioural contexts (Randall, 1989). These are indisputably signals: Footdrumming is sometimes produced in an undirected fashion (Randall, 1994), and playback experiments reveal that individuals discriminate between footdrumming of neighbours and strangers (Randall, 1994). What makes this a particularly illustrative example here is that no kangaroo rats are known to have modified morphology; the entire clade appears to exhibit only modified behaviour to produce these sounds as signals (J. Randall, personal communication). It would be interesting to know, in a phylogenetic context, what precursor behaviours gave rise to footdrumming.

Insect Wing Sound

Most arthropod sounds are produced by the integument, and thus fit the definition of locomotion-induced sounds used here. Many insect wing sounds are produced with modified morphology, such as the thickened veins of wings of butterflies (Yack, Otero, Dawson, Surlykke, & Fullard, 2000) or grasshoppers (Otte, 1970); or by clearly modified behaviour such as the wing songs of *Drosophila* (Spieth, 1974). One example is a test case for the modified behaviour criterion described above: wing sounds of midges and mosquitoes.

Male and female mosquitoes (*Aedes aegypti*) and midges (*Corsethrella appendiculata*) have different wing beat frequencies in ordinary flight, and the resulting wing hum is audible to both sexes. Males and unmated females modulate their wing beat frequency in response to the flight sound of the other sex. The result is that the female's third harmonic converges on the male's second harmonic in *Aedes* (Cator et al., 2009), or the fourth harmonic of females converges on the third harmonic of male midges (de Silva et al., 2015). Ordinary wing hum is an inevitable by-product of flight, and there is no modified morphology described. The adjustment of wing beat frequency is not a visual signal and does not appear to function in flight manoeuvrability or serve any flight-related function, suggesting that it is an acoustic signal. Thus, modulation of wing beat frequency constitutes modified behaviour. This example pushes against the limits of the idea of ‘voluntariness’ and ‘modified behaviour’ presented here, because in most respects this humming sound of the wing is entirely involuntary, with the animal's control of the sound limited to the frequency.

CONCLUSIONS

Several general observations are warranted. First, I have almost entirely ignored learning, despite the fact that learning could obviously play an important role in the communication function of locomotion-induced sounds, and complicate much of what is written here. Humans clap their hands as a sonation. It seems likely that learning has played a prominent role in both performance of this behaviour and also to associate this sound with a communication function. Second, the assessments above are in most cases based on limited knowledge, with the null that the sound in question is not functional. The results of the heuristic questions presented in Table S1, applied to a poorly studied species, is a hypothesis. Instances in which the diagnosis provided by the heuristic is wrong are also likely the most interesting cases to follow up with further study. For example, in the Introduction I claim that combustion engine noise is not a signal, and yet, like midge or mosquito wing sounds, revving a vehicle's engine can clearly be a signal (e.g. a threat display to some poor cyclist). Third, I have said little about effects of the putative signal on potential receivers. Studying effects in receivers is necessary to establish function.

Locomotion-induced sounds can be 'badly behaved' as signals. The clearest examples of animal signals are those in which the phenotypic character in question has an evolved form clearly linked specifically to elicit a response from a receiver, such as a bright colour patch or loud vocalization, and not to another function (Maynard Smith & Harper, 2003). Locomotion-induced sounds tend to be less clear, since essentially all animals are selected to locomote for nonsignalling function (Lotem et al., 1999). Even when locomotion itself is selected for signalling function, as in motor displays, the locomotion-induced sound is usually a part of multimodal display, in which the dominant modality may be visual. Disentangling the secondary modality from the primary modality of a multimodal display can be difficult. During human speech, are moving lips a visual signal? (What if the receiver is deaf?) Are the motions of a bird's beak or a frog's vocal sac during singing visual displays? Taylor, Klein, Stein, and Ryan (2008) studied the effects of motions of the vocal sac of singing male túngara frogs on receivers, but explicitly described the underlying motions of a frog vocal sac as a visual cue, not a signal, because the primary function of the vocal sac is to aid in singing.

There are many motion-induced sounds that are salient but are obviously not signals. Everyday human experience shows that every fidget, scratch or finger stroke on a keyboard makes sound. A strong wind through the branches of a pine tree produces a distinctive, ethereal, whooshing sound that is noteworthy to human ears. Are the trees talking to us? Although Pangloss (Gould & Lewontin, 1979) might argue that trees evolved cylindrical needles to make Aeolian tones for mammals to hear, it is obviously more reasonable to consider this sound as a physical by-product of air flowing fast past needles that have evolved to be cylindrical for other reasons. Since all motions make sound, locomotion-induced sounds of animals are a ubiquitous feature of locomotion. Most of these sounds are cues arising out of motions with a primary function that does not include producing sound. The null hypothesis is that these sounds, such as the purring engine of an approaching car or the footsteps of an approaching colleague, are a by-product. Within this milieu of motion-generated sound, signals are a special case.

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Supplementary Data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.anbehav.2018.07.009>

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