

# Robust rhythm reporting will advance ecological and evolutionary research

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## Abstract

1. Rhythmicity in the millisecond to second range is a fundamental building block of communication and coordinated movement. But how widespread are rhythmic capacities across species, and how did they evolve under different environmental pressures? Comparative research is necessary to answer these questions but has been hindered by limited crosstalk and comparability among results from different study species.
2. Most acoustics studies do not explicitly focus on characterising or quantifying rhythm, but many are just a few scrapes away from contributing to and advancing the field of comparative rhythm research. Here, we present an eight-level rhythm reporting framework which details actionable steps researchers can take to report rhythm-relevant metrics. Levels fall into two categories: metric reporting and data sharing. Metric reporting levels include defining rhythm-relevant metrics, providing point estimates of temporal interval variability, reporting interval distributions, and conducting rhythm analyses. Data sharing levels are: sharing audio recordings, sharing interval durations, sharing sound element start and end times, and sharing audio recordings *with* sound element start/end times.
3. Using sounds recorded from a sperm whale as a case study, we demonstrate how each reporting framework level can be implemented on real data. We also highlight existing best practice examples from recent research spanning multiple species. We clearly detail how engagement with our framework can be tailored case-by-case based on how much time and effort researchers are willing to contribute. Finally, we illustrate how reporting at any of the suggested levels will help advance comparative rhythm research.
4. This framework will actively facilitate a comparative approach to acoustic rhythms while also promoting cooperation and data sustainability. By quantifying and reporting rhythm metrics more consistently and broadly, new avenues of inquiry and several long-standing, big picture research questions become more tractable. These lines of research can inform not only about the behavioural ecology of animals but also about the evolution of rhythm-relevant phenomena and the behavioural neuroscience of rhythm production and perception. Rhythm is clearly

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an emergent feature of life; adopting our framework, researchers from different fields and with different study species can help understand why.

#### KEYWORDS

animal communication, bioacoustics, comparative approach, open science, reporting framework, rhythm, timing

## 1 | INTRODUCTION

From the rhythm of the tides to that of a beating heart, temporal structures that operate over different scales are frequently described as 'rhythmic'. What unites these and other examples (e.g. rhythm of the seasons, rhythm in music, rhythm in speech) is a recurrent, predictable pattern over time. For acoustic rhythms, this temporal pattern conveys information in and of itself, regardless of the features of the sound elements—notes, clicks, calls, pulses, songs and so forth—that are being repeated (Garcia et al., 2020; Gerhard, 2003; Margoliash, 1983; Williams & Staples, 1992). An example is human Morse code, where the precise combination of short sounds, long sounds, and silences codes for letters, numbers, punctuation, and words. In other taxa, the rhythmic patterning of signals can communicate signaller species (e.g. woodpeckers, Picidae family), signaller cultural group membership (e.g. sperm whales, *Physeter macrocephalus*) or predator threat urgency (e.g. meerkats, *Suricata suricatta*) (Garcia et al., 2020; Hersh et al., 2022; Manser, 2001). Rhythm is a fundamental feature of life and plays a critical role in acoustic communication for many species, but how the capacities underlying this remarkable ability evolved in human and non-human animals remains enigmatic.

To unveil this mystery, a growing number of researchers are investigating the acoustic rhythms of different taxa across behavioural contexts and with various aims. Rhythm analyses are used to better understand species discrimination, physiological correlates between communication and movement, mating preferences, and arousal coding (Burchardt et al., 2019; David et al., 2003; Demartsev et al., 2022; Manser, 2001; McRae, 2020; Norton & Scharff, 2016). Other contexts in which temporal structures play a substantial role include during multi-individual displays (e.g. conspecific duets and choruses) and vocal ontogeny (Chronister et al., 2023; Pika et al., 2018; Sasahara et al., 2015; Yoshida & Okanoya, 2005). Acoustic analyses often include quantification of rhythm-relevant temporal parameters, but inconsistent reporting of those parameters and minimal crosstalk across studies, taxa, and lines of research limit comparisons of results.

Many researchers have espoused the merits of studying different facets of animal acoustic communication—including vocal production learning, acoustic allometry, and song production—using comparative approaches (Bowling et al., 2017; Fitch, 2006; Garland & McGregor, 2020; Lattenkamp & Vernes, 2018; Martin et al., 2017; Ravnani et al., 2019; Rendell et al., 2021). Indeed, the volume of relevant papers published over the last decade indicates a growing

consensus that a productive way to advance the study of rhythm in (human and non-human) animal communication is through a cross-species, comparative approach.

To ensure that the comparative approach is feasible for research on rhythm in acoustic signals or other communication modalities, clear methodologies and comprehensible terminology are needed. The use of *clear methodologies* has been discussed in published 'primers' that illustrate different ways to quantify acoustic rhythms, ranging from simple measures of (deviation from) isochrony,<sup>1</sup> such as the coefficient of variation (CV) of temporal intervals, to more complex measures of hierarchical temporal structure, such as multifractal analysis of signal amplitude envelopes (Burchardt & Knörnschild, 2020; Kello et al., 2017; Kershenbaum et al., 2016; Ravnani & Norton, 2017; Roeske et al., 2018; Saar & Mitra, 2008). *Comprehensible terminology* does not necessarily mean universal definitions (c.f. Ravnani, 2017a): while terminology variation across disciplines or taxa is not an issue per se, it must be accounted for with clear definitions. As an example of this variability, consider the following subset of terms used in the literature to describe one of the most important units for rhythm analyses, an interval between two elements of interest: inter-bout interval, inter-call interval, inter-click interval, inter-onset interval (IOI), inter-pulse interval, inter-song interval, and more (Burchardt et al., 2019; Hersh et al., 2022; Herzing, 2015; Moran et al., 2020; Norton & Scharff, 2016; Schneider & Mercado III, 2019). There can be subtle differences in how these terms are defined, making comparisons across studies potentially flawed. Throughout this manuscript, we use the term 'interval' to mean the temporal duration between any points of interest in an acoustic sequence.

Different fields have access to the methods and terminology needed to conduct widespread analyses of acoustic rhythms but show little consistency in how and when techniques are applied and results reported. A comparative approach is thus feasible in theory, but not yet possible in practice, generating a 'reporting gap' in the literature.

Multiple factors contribute to this reporting gap. Crosstalk among bird, mammal, insect, fish and amphibian researchers is generally limited and, when it does occur, occurs unevenly (e.g. whale song is frequently compared to birdsong but rarely to cricket or frog song). Species that make rhythmically similar sounds using different production mechanisms are also rarely compared. For example, certain cricket and fish species produce isochronous sound sequences, but have not been compared because *how* they

do so—wing stridulation in the former and pulsatile calling in the latter—is very different (Burchardt, Picciulin, et al., 2021; Moran et al., 2020). Under similar pressures, however, convergent evolution can drive systems to similar endpoints via different mechanisms. Even neurally ‘simple’ oscillatory behaviour, like that seen in slime moulds *Physarum polycephalum* or nematodes *Caenorhabditis elegans*, can help us understand, for example, whether isochrony is an ancestral mode of animal rhythmic signalling (Fouad et al., 2018; Kobayashi et al., 2006). Quantifying and sharing rhythmic metrics for many different species is crucial to facilitating answers to such ‘big picture’ questions, but best practice reporting guidelines are missing.

Here, we present a reporting framework for research on acoustic rhythms. Many acoustic datasets are just a few scrapes away from contributing to and advancing the field of comparative rhythm research. Cognizant that researchers may have limited data, time, or interest, this framework outlines various degrees of data reporting, all of which will bolster future comparative work. Our goal for this framework is not to convert every researcher into a rhythm specialist, but rather to encourage and provide guidelines for reporting rhythm-relevant metrics in acoustics studies.

## 2 | REPORTING ON RHYTHM-RELEVANT PARAMETERS

Our reporting framework consists of eight levels, which can be divided into two categories: metric reporting (levels A–D, Box 1) and data sharing (levels E–H, Box 2) (Figure 1a). Box 3 illustrates how each level of the reporting framework can be applied using a real-world example. The ordering of levels within and across categories indicates a logical progression of analytical steps rather than absolute reporting priority. Generally speaking, the contributing researchers’ time expenditure, physical amount of data shared, and usefulness for subsequent users increases from level A to H. For example, level A likely corresponds to the least additional effort (in terms of time and other constraints) for contributing researchers, and least benefit for other colleagues interested in reusing the data. Level H likely requires greater additional effort and commitment because it involves sharing fully labelled and annotated recordings, but at the same time provides readily reusable data.

By labelling, we mean labels in the temporal domain that denote temporal points of interest in a recording, such as element start times, element end times, or peak amplitude instances. Each of these types of labels can be used to calculate intervals, which are the foundation for most rhythm analyses. In contrast to ‘labelling’, ‘annotating’ refers to adding descriptive notes to recordings, such as recording context or element type(s) (Figure 1b), ultimately leading to a list of descriptors. While audio recording processing is often still done manually, semi-automatic or automatic software that can aid in such processing, like Chipper or PAMGuard, are becoming increasingly popular (Gillespie et al., 2008; Searfoss et al., 2020).

Levels E–H of the reporting framework (Figure 1a) involve uploading data to a publicly accessible repository, such as Open Science Framework, Dryad Digital Repository, Mendeley Data, GitHub, Figshare, or Zenodo. This recommendation touches on two important topics in science: data sharing and data storage. Whether or not researchers share their data can depend on many factors, including funding body mandates, journal requirements, fear of being ‘scooped’, time constraints, and/or perceived helpfulness of doing so (Gomes et al., 2022). Even when researchers are able and willing to share data, dataset storage poses real challenges that scale up as the size of the dataset increases (e.g. repository costs, storage space limitations, energy consumption). Despite these challenges, open access data is key to scientific progress. The extensive benefits of open access data include: avoiding unnecessary redundancy, enabling replication, ensuring transparency, addressing inequity, promoting sustainability, and generally fostering goodwill and collaboration, rather than animosity and competition, among researchers (Gomes et al., 2022; Munafò et al., 2017; Popkin, 2019). For individual researchers, open access data can directly translate into more research citations and advance future work on one’s study system.

It is worth noting that the different levels in our reporting framework are separated by soft subdivisions rather than hard boundaries. Level A—labelling elements and defining metrics—is a prerequisite for most other levels. It can stand alone as a first step towards facilitating comparability, but if other levels are reported on, the elements and metrics must be reported on as well. For example, Level B—providing point estimates of temporal interval variability—requires knowledge of the elements and metrics that were used to quantify intervals. From a comparative perspective, the acoustic sequence ‘metadata’ mentioned in Box 2 with regards to Level F—sharing interval data—would ideally be shared at all other reporting levels as well, as it can add key nuance to downstream analyses and interpretations. This includes sharing as much information as possible regarding the individual, group, and/or species identity of the recorded animal(s); the behavioural context in which the recording was made (e.g. mating, dominance display, predator threat, etc.); and the general time scale, given that acoustic communication of different taxa can happen over vastly different time scales (days, hours, minutes, seconds, etc.). As these examples illustrate, there are areas of overlap among the different reporting levels, and reporting at any of the suggested levels will help advance ecological and evolutionary research. We have devised a decision tree to guide researchers in deciding which rhythm relevant metrics to report and how best to do so (Figure 1c).

## 3 | LOOKING AHEAD

By quantifying and reporting metrics more consistently as we suggest, questions in animal rhythmicity become more tractable. Answering these questions can inform not only about the behavioural ecology of animals, but also about the cognitive neuroscience of rhythm production and perception and the evolution of rhythm-relevant phenomena.

## BOX 1 Metric reporting

### LEVEL A: Label elements and define metrics

During acoustic analyses, sound elements are often labelled or annotated in some way, even when no specific temporal parameters are quantified. If those markings can be extracted as labelled timepoints this can be a straightforward (and requisite) first step for further rhythm-relevant analysis. To enable comparisons across studies, it is crucial to clearly define the kind of interval that was labelled. For example, the abbreviation 'ICI' is polysemous across studies, alternately being used to refer to inter-click intervals (typically the duration between the start of one click and the start of the next click) or inter-call intervals (often considered the duration between the end of one call and the start of the next call).

### LEVEL B: Provide point estimates

Reporting temporal interval variability parameters can be quick but highly informative. The mean, standard deviation (SD), median, and range of intervals are informative metrics that are useful and often essential in subsequent analyses and comparisons. The CV, typically reported as a percentage, can be calculated by dividing the SD by the mean when these two quantities are well-defined. It is independent of sample size and the mean, making it a powerful measure for comparing rhythmic variability across studies. Finding drivers behind documented variability or consistency can help researchers better understand the importance of rhythmic structures within and across species' communication systems. Here, it is crucial to describe over which time scales and/or for which intervals point estimates were calculated or reported. For example: were parameters calculated or summarised per sound sequence, per individual, per age class, per population, per day, and so forth?

### LEVEL C: Report interval distribution estimates

Distributional information is partly lost when only reporting basic statistics (Ravnani, 2017b). A next step is to report the distribution of labelled intervals or other temporal parameters. This can be conveyed visually (via histograms) or descriptively—does the data follow a Gaussian distribution, bimodal distribution or uniform distribution? These descriptions provide clues about underlying rhythms: a uniform distribution suggests there are no distinct rhythmic categories in the dataset, a bimodal distribution potentially suggests several different rhythm categories, and a steep unimodal distribution indicates an isochronous rhythm.

### LEVEL D: Do a rhythm analysis

The final metric reporting level addresses specific rhythm questions using an appropriate method (or methods). Many types of rhythm analyses are possible, and have been discussed at length in the literature (Burchardt, Briefer, et al., 2021; De Gregorio et al., 2021; Ravnani & Norton, 2017; Roeske et al., 2018; Saar & Mitra, 2008; Sasahara et al., 2015; Schneider & Mercado III, 2019). For example, the underlying rhythmic beat of an acoustic sequence can be automatically calculated ([https://github.com/LSBurchardt/R\\_app\\_rhythm/tree/master/RhythmAnalysis](https://github.com/LSBurchardt/R_app_rhythm/tree/master/RhythmAnalysis)) using methods from Burchardt and Knörnschild (2020). Given that different rhythm analyses target different aspects of rhythm, researchers will use and report results from multiple complementary approaches in the best-case scenario.

## 3.1 | Rhythm and ecology

Rhythm research can help us better understand the behavioural ecology of different species. Different environments present different challenges for animals that communicate acoustically, and can lead to different degrees of information encoding in temporal versus spectral features of acoustic signals (Kershenbaum et al., 2016). For example, songbirds that live in open habitats, like grasslands, exhibit greater temporal resolution in rapidly modulated calls than songbirds that live in reverberant habitats, like forests (Henry & Lucas, 2010). Similar trends are seen when comparing temporal features of echolocation when bats are foraging in open versus cluttered environments (Petrites et al., 2009; Stidsholt et al., 2021; Wund, 2006). A testable hypothesis emerging from these studies—and which would benefit from cross-species researchers adopting our reporting framework—is that

open-habitat species show greater rhythmic complexity in their signals than reverberant- or cluttered-habitat species. This hypothesis can be extended beyond songbirds and bats; for example, by comparing the vocalisations of coastal versus open-ocean fish or cetacean species.

The temporal structure of acoustic signals can also provide information about another ecological factor, namely temperature. In two-spotted crickets *Gryllus bimaculatus*, repetition rates of chirps show a linear increase for temperatures between 15 and 24°C, and females tend to only react to male songs with rates that match their own temperature conditions (Doherty, 1985). This suggests a connection between the physiological mechanisms underlying pattern generation and pattern recognition in crickets. In some ectothermic fish species, where communicative sounds are produced by sonic muscle contractions (which in turn are highly influenced by temperature), repetition rates of within-sound elements

## BOX 2 Data sharing

### LEVEL E: Share audio recordings

Sharing unprocessed audio recordings, such as .wav files, grants considerable flexibility to other researchers who want to repurpose a dataset for different analyses (for example, by allowing other researchers to focus on other sound elements). Apart from storage space constraints, this reporting level typically does not require high time investment from contributing researchers. Large audio datasets can be downsampled to decrease file size without compromising future rhythm analyses, as temporal features are generally robust to moderate downsampling (Kottege et al., 2012). Alternatively, intensity curves of the data rather than the actual audio recordings could be shared. A fast and accessible option to extract intensity curves is implemented in Parselmouth, a Python library for the Praat software (<https://github.com/YannickJadoul/Parselmouth>) (Jadoul et al., 2017). However, certain types of information are lost when utilising this approach, and we therefore do not advise it for some situations (e.g. for recordings with multiple individuals or element types).

### LEVEL F: Share interval data

Interval data can also be shared in a publicly accessible database. From this type of data, other researchers can calculate interval means and SDs (Level B), generate interval distributions (Level C), or run specific rhythm analyses (Level D). It is critical to describe the intervals being shared in detail. This includes providing sequence definitions, the labelled points of interest in each sequence (e.g. element start times, element end times, element peak amplitudes), and metadata for each sequence (e.g. recorded individual, context).

### LEVEL G: Share element start and end times

Labelling and annotating acoustic recordings is typically the most time-consuming stage in any analytical pipeline. Therefore, sharing data on labelled sequential sound points of interest (i.e. element start and end times) as well as corresponding annotations (if available) affords immense flexibility in re-analysis. Doing so allows other researchers to calculate the intervals of interest, the durations of sound elements, and the durations of silences. This can help us better understand acoustic communication in species that produce sound elements that vary in duration, such as skylarks and humpback whales (Allen et al., 2017; Briefer et al., 2008).

### LEVEL H: Share recordings and element labels

The most comprehensive level of data sharing combines levels E and G, where recordings and the associated time labels and annotations are shared. This enables researchers to run any kind of temporal analysis they like, while providing the necessary expertise (i.e. in annotating) to ensure high quality research.

(i.e. pulses) are also positively correlated with temperature (Ladich, 2018). Have some species evolved ways to escape this temperature-dependency in their signalling behaviour? How do different temperatures influence the temporal structure of vocalisations, and which animals are able to infer environmental information from that structure? Answering these questions becomes increasingly possible under our reporting framework and can help establish connections between rhythms and the socio-ecological contexts in which they are produced.

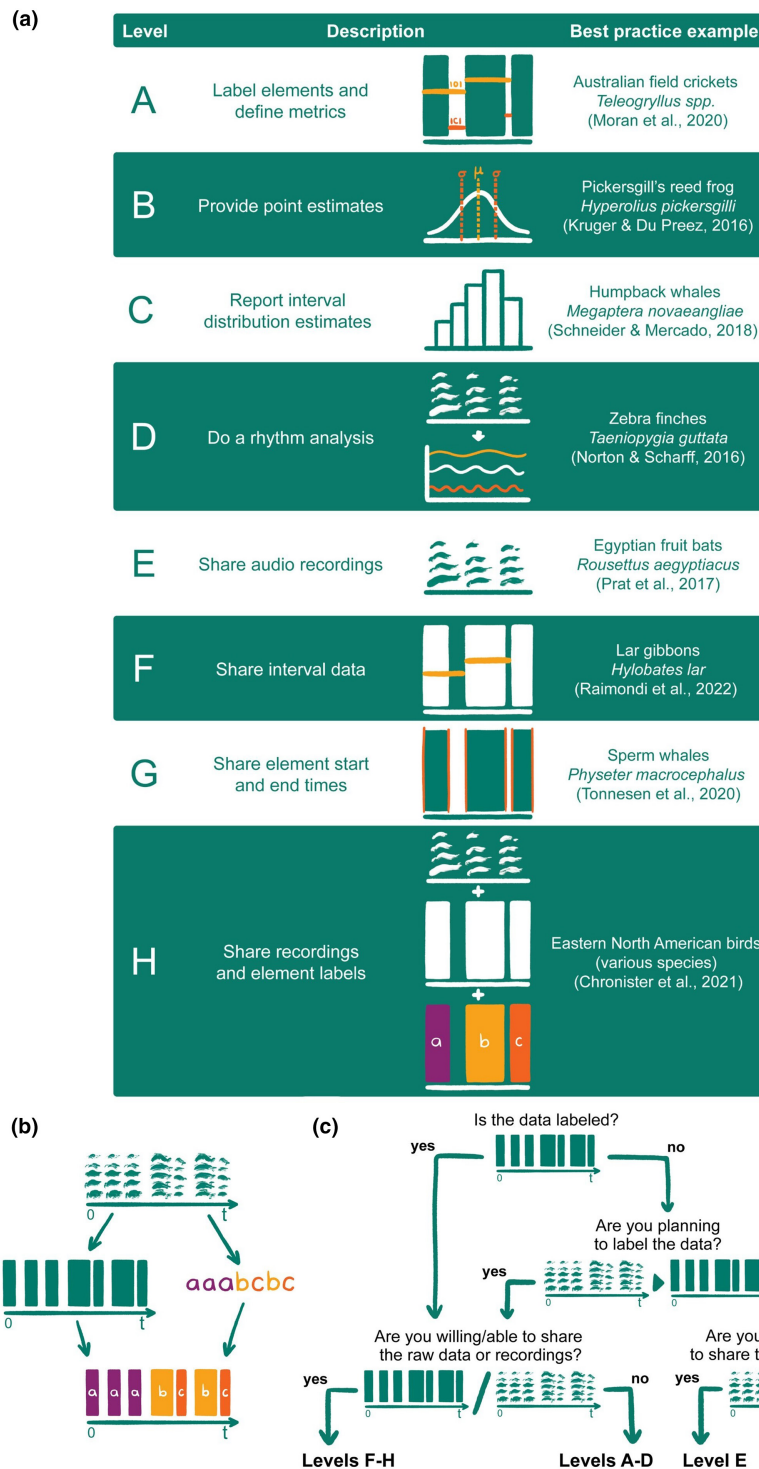
## 3.2 | Rhythm and behaviour

The power of rhythm to modulate animal behaviour is perhaps best illustrated by cases where seemingly small rhythmic alterations have large effects on subsequent behaviour and fitness. For example, male northern elephant seals *Mirounga angustirostris* can distinguish other males based on subtle differences in tempo and timbre of threat calls (Mathevon et al., 2017). This individual recognition, presumably facilitated by rhythm perception, has direct behavioural consequences; in a playback experiment, males were significantly more likely to approach the speaker if the broadcasted threat call came from a subordinate male, but not if the call came from a dominant male. Recent work on rock hyraxes *Procapra capensis* has shown that males who sing more isochronous songs have higher reproductive success (Demartsev et al., 2022). As these examples illustrate, structuring of the silences in acoustic displays can be just as (or more) important than specific features of vocalisations themselves when it comes to information encoding and conspecific decision-making. Understanding the temporal structure of communication signals from single individuals is a requisite stepping stone to understanding more complex conspecific interactions and behaviours, such as vocal overlapping and turn-taking (Ravignani et al., 2014).

## 3.3 | Rhythm and neuroscience

Rhythmicity in neuroscience is already an extremely rich field on its own (e.g. Buzsaki, 2006). Metrics to measure rhythmicity in neural activity partly differ from, and have developed in parallel with, behavioural measures of rhythmicity (Ermentrout et al., 2008; Kałuzny & Tarnecki, 1993; Okobi Jr et al., 2019; Reinhart & Nguyen, 2019). At an even more fundamental level, neural rhythmicity is measured on continuous, oscillatory signals (i.e. waves) while the acoustic rhythmicity we focus on here deals with point events in time. Nevertheless, our framework is interesting for the field of neuroscience, too. For example, an application for cognitive neuroscience would be in quantitative meta-analyses: if several studies report rhythmic metrics for acoustic behavioural stimuli together with neural measurements, one could correlate the two across studies. Moreover, there is some evidence that the neural mechanisms for the perception of rhythm are conserved across species, including humans (Darwin, 1872; Hulse et al., 1995; Klump & Maier, 1989;





**FIGURE 1** Reporting framework visual guide and key concepts. (a) Overview of reporting framework levels (for more details, see Section 2 and Boxes 1 and 2). For each level, a 'best practice' example is provided (Chronister et al., 2021; Kruger & Du Preez, 2016; Moran et al., 2020; Norton & Scharff, 2016; Prat et al., 2017; Raimondi et al., 2023; Schneider & Mercado III, 2019; Tønnesen et al., 2020). (b) A toy example, showing how a sound spectrogram (top) can be temporally labelled (by marking the start and end points of elements; middle left, dark green boxes), annotated (by marking element information, such as element type; middle right, coloured letters), or both (bottom). (c) This decision tree can help users determine which level of reporting is most suitable for their specific situation.

Knudsen & Gentner, 2010; Patel & Iversen, 2014). Therefore, a comparative approach to rhythm analysis in animal communication can be a powerful tool for studying the neural underpinnings of rhythm

production and perception. Those involve a complex interplay between neural oscillators and cognitive processes such as attention and memory (Golumbic et al., 2013; Lakatos et al., 2008). The

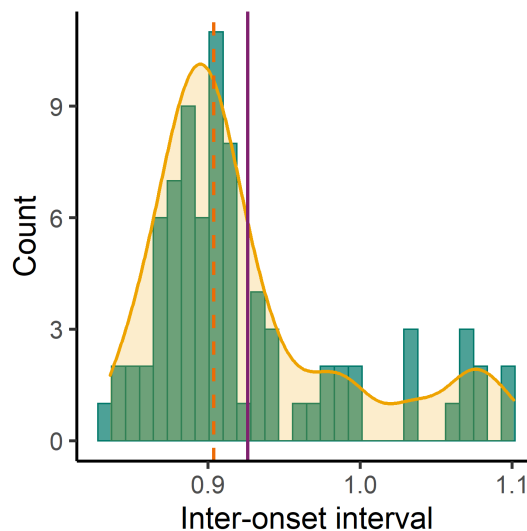
### BOX 3 Applying the framework to a recording of sperm whale echolocation

To illustrate how our reporting framework can be applied to real acoustic data, we use an audio file of echolocation clicks recorded from a single sperm whale off the Galápagos Islands on 11 March 2013. The elements of interest are clicks and the metric of interest is the click IOI (i.e. the time between the start of one click and the start of the subsequent click; Level A). The start time of each click is manually labelled. Sperm whale echolocation clicks are multipulsed, and click decay makes determining click end times challenging (Zimmer et al., 2005). For that reason, we have not quantified click end times. All parameters are calculated for and representative of the single audio file. The average IOI duration is 0.926 s (median=0.904 s; range=0.836–1.10 s) with a standard deviation of 0.067 s, yielding a CV of 7.2% (Level B). The low CV suggests that the echolocation clicks in the recording are generally isochronously spaced. A histogram showing the distribution of IOIs (Figure 2) is right-skewed, with a density peak closer to the median IOI value than to the mean IOI value (Level C). Using the open source RANTO software ([https://github.com/LSBurchardt/R\\_app\\_rhythm/tree/master/RhythmAnalysis](https://github.com/LSBurchardt/R_app_rhythm/tree/master/RhythmAnalysis)), we determine the isochronous rhythm that best matches the clicks in the recording using the IOI approach (where the median interval length is transformed into a frequency) and the Fourier approach (where the interval sequence is decomposed into its sinusoidal components) (Level D). Both approaches return a best fitting isochronous beat of 1.11 Hz. Following established methods for quantifying the relationship among adjacent IOIs (De Gregorio et al., 2021; Raimondi et al., 2023; Roeske et al., 2020), we find an average ratio of adjacent IOIs of 0.500, which corresponds to an isochronous sequence (Level D). The audio recording (.wav format; Level E), interval data (.csv format; Level F), click start times (.csv format, Level G), and recording specifications can be freely accessed via the Open Science Framework (<https://osf.io/jnpqh/>) (collectively, Level H).

analysis of acoustic rhythms can shed light on these processes by revealing the temporal structure of sensory inputs and the neural responses to these inputs.

### 3.4 | Rhythm and evolution

In order to estimate the most likely rhythmic ancestral state of sound production or to construct cross-species phylogenies of rhythmic abilities, we must first understand the temporal structure of sound production for phylogenetically-distinct species (Garcia et al., 2020;



**FIGURE 2** Histogram (dark green) and density plot (gold) of click IOIs (in seconds) from a recording of an echolocating sperm whale. The mean IOI is denoted by the solid purple line and the median IOI by the dashed orange line.

Ravignani & Madison, 2017; Terhune, 2019). Our framework encourages this type of fundamental research which, if reported, will allow researchers to tackle questions such as whether similar rhythmic abilities in different species are analogous or homologous.

Additionally, rhythmic capabilities and their evolution are likely coupled to other phenomena. For example, vocal production learning—the ability to acquire new vocalisations or modify existing vocalisations based on experience—has been linked to flexible rhythm pattern perception in songbirds and seals (Rouse et al., 2021; Verga et al., 2022). Other phenomena, such as entrainment and synchrony, are also closely linked to rhythm production and perception in various taxa, including insects, frogs, birds, and humans (Bowling et al., 2013; Filer et al., 2021; Hartbauer & Roemer, 2016; Ten Cate &

### BOX 4 Outstanding questions

- Is isochrony an ancestral mode of rhythm production within the animal phylogeny, or did isochronous signals evolve independently in different taxa?
- How does rhythm production vary across individuals, groups, or species, and what does this variation tell us about rhythm function?
- Which selective pressures promote rhythmic vs. arrhythmic sound production?
- How do different production mechanisms shape rhythms?
- Which factors (e.g. neurobiology, gross anatomy) influence the flexibility of rhythm production?
- How is the complexity of rhythm production connected to the cognitive and perceptual abilities of a species?

Spierings, 2019). That rhythm is implicated in such a diversity of processes suggests that rhythm and other abilities may have coevolved. Rigorous testing of coevolutionary hypotheses versus alternative explanations will be greatly facilitated by more consistent reporting of rhythm-relevant metrics in bioacoustics studies.

## 4 | CONCLUDING REMARKS

Throughout the animal communication literature, many published datasets are just a few small steps away from easy integration into comparative rhythm analyses. The rhythm reporting framework for research on acoustic communication presented here aims to standardise rhythm metric reporting and foster multi-disciplinary and cross-species comparisons. It comprises eight levels that require varying degrees of time investment, data resolution, and researcher interest. Our framework touches on timely issues in science, including data transparency, accessibility and sustainability, and echoes a growing body of work calling for more open and equitable scientific practices. By embracing this framework, researchers can help answer several long-standing, 'big picture' questions in rhythm and animal communication research (Box 4). Rhythm is clearly an emergent feature of life; using our framework, researchers from different fields and with different study species can help understand why.

### AUTHOR CONTRIBUTIONS

Taylor A. Hersh and Lara S. Burchardt conceived the idea, analysed the audio recording included in Box 3, and managed the project. All authors contributed critically to manuscript drafting and editing and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to declare.

### PEER REVIEW

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### DATA AVAILABILITY STATEMENT

The sperm whale echolocation file and its associated data following the rhythm reporting framework can be accessed via the Open

Science Framework (<https://osf.io/jnpqh/>). We used the open source RANTO software for rhythm analyses ([https://github.com/LSBurchardt/R\\_app\\_rhythm/tree/master/RhythmAnalysis](https://github.com/LSBurchardt/R_app_rhythm/tree/master/RhythmAnalysis)).

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### ENDNOTE

<sup>1</sup> Isochronous rhythms are those where elements are separated by intervals of equal duration. For example, metronomes and analogue clocks produce isochronous sounds.

### REFERENCES

- Allen, J. A., Murray, A., Noad, M. J., Dunlop, R. A., & Garland, E. C. (2017). Using self-organizing maps to classify humpback whale song units and quantify their similarity. *The Journal of the Acoustical Society of America*, 142(4), 1943–1952. <https://doi.org/10.1121/1.4982040>
- Bowling, D. L., Garcia, M., Dunn, J. C., Ruprecht, R., Stewart, A., Frommolt, K.-H., & Fitch, W. T. (2017). Body size and vocalization in primates and carnivores. *Scientific Reports*, 7(1), 1–11.
- Bowling, D. L., Herbst, C. T., & Fitch, W. T. (2013). Social origins of rhythm? Synchrony and temporal regularity in human vocalization. *PLoS ONE*, 8(11), e80402. <https://doi.org/10.1371/journal.pone.0080402>
- Briefer, E., Aubin, T., Lehongre, K., & Rybak, F. (2008). How to identify dear enemies: The group signature in the complex song of the skylark *Alauda arvensis*. *Journal of Experimental Biology*, 211(3), 317–326.
- Burchardt, L. S., Briefer, E. F., & Knörnschild, M. (2021). Novel ideas to further expand the applicability of rhythm analysis. *Ecology and Evolution*, 11(24), 18229–18237.
- Burchardt, L. S., & Knörnschild, M. (2020). Comparison of methods for rhythm analysis of complex animals' acoustic signals. *PLoS Computational Biology*, 16(4), e1007755. <https://doi.org/10.1371/journal.pcbi.1007755>
- Burchardt, L. S., Norton, P., Behr, O., Scharff, C., & Knörnschild, M. (2019). General isochronous rhythm in echolocation calls and social vocalizations of the bat *Saccopteryx bilineata*. *Royal Society Open Science*, 6(1). <https://doi.org/10.1098/rsos.181076>
- Burchardt, L. S., Picciulin, M., Parmentier, E., & Bolgan, M. (2021). A primer on rhythm quantification for fish sounds: A Mediterranean case study. *Royal Society Open Science*, 8(9), 210494.
- Buzsaki, G. (2006). *Rhythms of the brain*. Oxford University Press.
- Chronister, L. M., Rhinehart, T. A., & Kitzes, J. (2023). When birds sing at the same pitch, they avoid singing at the same time. *Ibis*. <https://doi.org/10.1111/ibi.13192>
- Chronister, L. M., Rhinehart, T. A., Place, A., & Kitzes, J. (2021). *An annotated set of audio recordings of eastern north American birds containing frequency, time, and species information*. Wiley Online Library.
- Darwin, C. (1872). *The descent of man, and selection in relation to sex* (Vol. 2). D. Appleton.
- David, J. A. d. O., Zefa, E., & Fontanetti, C. S. (2003). Cryptic species of *Gryllus* in the light of bioacoustic (Orthoptera: Gryllidae). *Neotropical Entomology*, 32, 75–80.
- De Gregorio, C., Valente, D., Raimondi, T., Torti, V., Miaretsoa, L., Friard, O., Giacomini, C., Ravnani, A., & Gamba, M. (2021). Categorical rhythms in a singing primate. *Current Biology*, 31(20), R1379–R1380.
- Demartsev, V., Haddas-Sasson, M., Ilany, A., Koren, L., & Geffen, E. (2022). Male rock hyraxes that maintain an isochronous song rhythm achieve higher reproductive success. *Journal of Animal Ecology*. <https://doi.org/10.1111/1365-2656.13801>



- Doherty, J. A. (1985). Temperature coupling and 'trade-off' phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* De Geer (Gryllidae). *Journal of Experimental Biology*, 114(1), 17–35.
- Ermentrout, G. B., Galán, R. F., & Urban, N. N. (2008). Reliability, synchrony and noise. *Trends in Neurosciences*, 31(8), 428–434.
- Filer, A., Burchardt, L. S., & van Rensburg, B. J. (2021). Assessing acoustic competition between sibling frog species using rhythm analysis. *Ecology and Evolution*, 11(13), 8814–8830.
- Fitch, W. T. (2006). The biology and evolution of music: A comparative perspective. *Cognition*, 100(1), 173–215.
- Fouad, A. D., Teng, S., Mark, J. R., Liu, A., Alvarez-Illera, P., Ji, H., Du, A., Bhirgoo, P. D., Cornblath, E., & Guan, S. A. (2018). Distributed rhythm generators underlie *Caenorhabditis elegans* forward locomotion. *eLife*, 7, e29913.
- Garcia, M., Theunissen, F., Sèbe, F., Clavel, J., Ravnigani, A., Marin-Cudraz, T., Fuchs, J., & Mathevon, N. (2020). Evolution of communication signals and information during species radiation. *Nature Communications*, 11(1), 1–15. <https://doi.org/10.1038/s41467-020-18772-3>
- Garland, E. C., & McGregor, P. K. (2020). Cultural transmission, evolution, and revolution in vocal displays: Insights from bird and whale song. *Frontiers in Psychology*, 11, 2387. <https://doi.org/10.3389/fpsyg.2020.544929>
- Gerhard, D. (2003). Silence as a cue to rhythm in the analysis of speech and song. *Canadian Acoustics*, 31(3), 22–23.
- Gillespie, D., Mellinger, D. K., Gordon, J., McLaren, D., Redmond, P., McHugh, R., Trinder, P. W., Deng, X. Y., & Thode, A. (2008). PAMGUARD: Semiautomated, open source software for real-time acoustic detection and localisation of cetaceans. *Journal of the Acoustical Society of America*, 30(5), 54–62.
- Golumbic, E. M. Z., Ding, N., Bickel, S., Lakatos, P., Schevon, C. A., McKhann, G. M., Goodman, R. R., Emerson, R., Mehta, A. D., & Simon, J. Z. (2013). Mechanisms underlying selective neuronal tracking of attended speech at a 'cocktail party'. *Neuron*, 77(5), 980–991.
- Gomes, D. G. E., Pottier, P., Crystal-Ornelas, R., Hudgins, E. J., Foroughirad, V., Sánchez-Reyes, L. L., Turba, R., Martínez, P. A., Moreau, D., & Bertram, M. G. (2022). Why don't we share data and code? Perceived barriers and benefits to public archiving practices. *Proceedings of the Royal Society B: Biological Sciences*, 289(1987), 20221113.
- Hartbauer, M., & Roemer, H. (2016). Rhythm generation and rhythm perception in insects: The evolution of synchronous choruses. *Frontiers in Neuroscience*, 10, 223.
- Henry, K. S., & Lucas, J. R. (2010). Habitat-related differences in the frequency selectivity of auditory filters in songbirds. *Functional Ecology*, 24(3), 614–624.
- Hersh, T. A., Gero, S., Rendell, L., Cantor, M., Weigart, L., Amano, M., Dawson, S. M., Slooten, E., Johnson, C. M., Kerr, I., Payne, R., Rogan, A., Andrews, O., Ferguson, E. L., Hom-Weaver, C. A., Norris, T. F., Barkley, Y. M., Merckens, K. P., Oleson, E. M., ... Whitehead, H. (2022). Evidence from sperm whale clans of symbolic marking in non-human cultures. *Proceedings of the National Academy of Sciences of the United States of America*, 119(37), e2201692119. <https://doi.org/10.1073/pnas.2201692119>
- Herzing, D. (2015). Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in The Bahamas. *Animal Behavior and Cognition*, 2(1), 14–29. <https://doi.org/10.12966/abc.02.02.2015>
- Hulse, S. H., Bernard, D. J., & Braaten, R. F. (1995). Auditory discrimination of chord-based spectral structures by European starlings (*Sturnus vulgaris*). *Journal of Experimental Psychology: General*, 124(4), 409–423.
- Jadoul, Y., Thompson, B., & Boer, B. d. (2017). Introducing Parselmouth: A python interface to Praat. *Journal of Phonetics*, 71, 1–15. <https://doi.org/10.1016/j.wocn.2018.07.001>
- Kałużny, P., & Tarnecki, R. (1993). Recurrence plots of neuronal spike trains. *Biological Cybernetics*, 68(6), 527–534.
- Kello, C. T., Bella, S. D., Médé, B., & Balasubramaniam, R. (2017). Hierarchical temporal structure in music, speech and animal vocalizations: Jazz is like a conversation, humpbacks sing like hermit thrushes. *Journal of the Royal Society Interface*, 14(135), 20170231. <https://doi.org/10.1098/rsif.2017.0231>
- Kershenbaum, A., Blumstein, D. T., Roch, M. A., Akçay, Ç., Backus, G., Bee, M. A., Bohn, K., Cao, Y., Carter, G., Cäsar, C., Coen, M., Deruiter, S. L., Doyle, L., Edelman, S., Ferrer-i-Cancho, R., Freeberg, T. M., Garland, E. C., Gustison, M., Harley, H. E., ... Zamora-Gutierrez, V. (2016). Acoustic sequences in non-human animals: A tutorial review and prospectus. *Biological Reviews*, 91(1), 13–52. <https://doi.org/10.1111/brv.12160>
- Klump, G. M., & Maier, E. H. (1989). Gap detection in the starling (*Sturnus vulgaris*) I. Psychophysical thresholds. *Journal of Comparative Physiology A*, 164(4), 531–538.
- Knudsen, D. P., & Gentner, T. Q. (2010). Mechanisms of song perception in oscine birds. *Brain and Language*, 115(1), 59–68.
- Kobayashi, R., Tero, A., & Nakagaki, T. (2006). Mathematical model for rhythmic protoplasmic movement in the true slime mold. *Journal of Mathematical Biology*, 53(2), 273–286.
- Kottege, N., Kroon, F., Jurdak, R., & Jones, D. (2012). Classification of underwater broadband bio-acoustics using spectro-temporal features. *Proceedings of the Seventh ACM International Conference on Underwater Networks and Systems*, 1–8.
- Kruger, D. J. D., & Du Preez, L. H. (2016). The effect of airplane noise on frogs: A case study on the critically endangered Pickersgill's reed frog (*Hyperolius pickersgilli*). *Ecological Research*, 31(3), 393–405.
- Ladich, F. (2018). Acoustic communication in fishes: Temperature plays a role. *Fish and Fisheries*, 19(4), 598–612.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C. E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, 320(5872), 110–113. <https://doi.org/10.1126/science.1154735>
- Lattenkamp, E. Z., & Vernes, S. C. (2018). Vocal learning: A language-relevant trait in need of a broad cross-species approach. *Current Opinion in Behavioral Sciences*, 21, 209–215. <https://doi.org/10.1016/j.cobeha.2018.04.007>
- Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268(1483), 2315–2324.
- Margoliash, D. (1983). Acoustic parameters underlying the responses of song-specific neurons in the white-crowned sparrow. *Journal of Neuroscience*, 3(5), 1039–1057. <https://doi.org/10.1523/jneurosci.03-05-01039.1983>
- Martin, K., Tucker, M. A., & Rogers, T. L. (2017). Does size matter? Examining the drivers of mammalian vocalizations. *Evolution*, 71(2), 249–260.
- Mathevon, N., Casey, C., Reichmuth, C., & Charrier, I. (2017). Northern elephant seals memorize the rhythm and timbre of their rivals' voices. *Current Biology*, 27(15), 2352–2356. <https://doi.org/10.1016/j.cub.2017.06.035>
- McRae, T. R. (2020). A review of squirrel alarm-calling behavior: What we know and what we do not know about how predator attributes affect alarm calls. *Animal Behavior and Cognition*, 7(2), 168–191.
- Moran, P. A., Hunt, J., Mitchell, C., Ritchie, M. G., & Bailey, N. W. (2020). Sexual selection and population divergence III: Interspecific and intraspecific variation in mating signals. *Journal of Evolutionary Biology*, 33(7), 990–1005. <https://doi.org/10.1111/jeb.13631>
- Munafò, M. R., Nosek, B. A., Bishop, D. V. M., Button, K. S., Chambers, C. D., Percie du Sert, N., Simonsohn, U., Wagenmakers, E.-J., Ware, J. J., & Ioannidis, J. (2017). A manifesto for reproducible science. *Nature Human Behaviour*, 1(1), 1–9.
- Norton, P., & Scharff, C. (2016). 'Bird song metronomics': Isochronous organization of zebra finch song rhythm. *Frontiers in Neuroscience*, 10, 309. <https://doi.org/10.3389/fnins.2016.00309>
- Okobi, D. E., Jr., Banerjee, A., Matheson, A. M. M., Phelps, S. M., & Long, M. A. (2019). Motor cortical control of vocal interaction in neotropical singing mice. *Science*, 363(6430), 983–988.

- Patel, A. D., & Iversen, J. R. (2014). The evolutionary neuroscience of musical beat perception: The action simulation for auditory prediction (ASAP) hypothesis. *Frontiers in Systems Neuroscience*, 8, 57.
- Petrites, A. E., Eng, O. S., Mowlds, D. S., Simmons, J. A., & DeLong, C. M. (2009). Interpulse interval modulation by echolocating big brown bats (*Eptesicus fuscus*) in different densities of obstacle clutter. *Journal of Comparative Physiology A*, 195(6), 603–617.
- Pika, S., Wilkinson, R., Kendrick, K. H., & Veres, S. C. (2018). Taking turns: Bridging the gap between human and animal communication. *Proceedings of the Royal Society B: Biological Sciences*, 285(1880), 20180598.
- Popkin, G. (2019). Data sharing and how it can benefit your scientific career. *Nature*, 569(7756), 445–447.
- Prat, Y., Taub, M., Pratt, E., & Yovel, Y. (2017). An annotated dataset of Egyptian fruit bat vocalizations across varying contexts and during vocal ontogeny. *Scientific Data*, 4(1), 1–7.
- Raimondi, T., Di Panfilo, G., Pasquali, M., Zarantonello, M., Favaro, L., Savini, T., Gamba, M., & Ravignani, A. (2023). Isochrony and rhythmic interaction in ape duetting. *Proceedings of the Royal Society B: Biological Sciences*, 290(1990), 20222244.
- Ravignani, A. (2017a). Interdisciplinary debate: Agree on definitions of synchrony [correspondence]. *Nature*, 545, 158.
- Ravignani, A. (2017b). Visualizing and interpreting rhythmic patterns using phase space plots. *Music Perception*, 34(5), 557–568.
- Ravignani, A., Bowling, D., & Fitch, W. T. (2014). Chorusing, synchrony, and the evolutionary functions of rhythm. *Frontiers in Psychology*, 5, 1–15. <https://doi.org/10.3389/fpsyg.2014.01118>
- Ravignani, A., Dalla Bella, S., Falk, S., Kello, C. T., Noriega, F., & Kotz, S. A. (2019). Rhythm in speech and animal vocalizations: A cross-species perspective. *Annals of the New York Academy of Sciences*, 1453, 79–98. <https://doi.org/10.1111/nyas.14166>
- Ravignani, A., & Madison, G. (2017). The paradox of isochrony in the evolution of human rhythm. *Frontiers in Psychology*, 8, 1820. <https://doi.org/10.3389/fpsyg.2017.01820>
- Ravignani, A., & Norton, P. (2017). Measuring rhythmic complexity: A primer to quantify and compare temporal structure in speech, movement, and animal vocalizations. *Journal of Language Evolution*, 2(1), 4–19. <https://doi.org/10.1093/jole/lzx002>
- Reinhart, R. M. G., & Nguyen, J. A. (2019). Working memory revived in older adults by synchronizing rhythmic brain circuits. *Nature Neuroscience*, 22(5), 820–827.
- Rendell, L., Doolittle, E. L., Garland, E. C., & South, A. (2021). A boldly comparative approach will strengthen co-evolutionary accounts of musicality's origins. *Behavioral and Brain Sciences*, 44, e89.
- Roeske, T. C., Kelty-Stephen, D., & Wallot, S. (2018). Multifractal analysis reveals music-like dynamic structure in songbird rhythms. *Scientific Reports*, 8(1), 1–15. <https://doi.org/10.1038/s41598-018-22933-2>
- Roeske, T. C., Tchernichovski, O., Poeppel, D., & Jacoby, N. (2020). Categorical rhythms are shared between songbirds and humans. *Current Biology*, 30(18), 3544–3555. <https://doi.org/10.1016/j.cub.2020.06.072>
- Rouse, A. A., Patel, A. D., & Kao, M. H. (2021). Vocal learning and flexible rhythm pattern perception are linked: Evidence from songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, 118(29). <https://doi.org/10.1073/pnas.2026130118>
- Saar, S., & Mitra, P. P. (2008). A technique for characterizing the development of rhythms in bird song. *PLoS ONE*, 3(1), 1–6. <https://doi.org/10.1371/journal.pone.0001461>
- Sasahara, K., Tchernichovski, O., Takahashi, M., Suzuki, K., & Okanoya, K. (2015). A rhythm landscape approach to the developmental dynamics of birdsong. *Journal of the Royal Society Interface*, 12(112), 20150802.
- Schneider, J. N., & Mercado, E., III. (2019). Characterizing the rhythm and tempo of sound production by singing whales. *Bioacoustics*, 28(3), 239–256. <https://doi.org/10.1080/09524622.2018.1428827>
- Searfoss, A. M., Pino, J. C., & Creanza, N. (2020). Chipper: Open-source software for semi-automated segmentation and analysis of birdsong and other natural sounds. *Methods in Ecology and Evolution*, 11(4), 524–531.
- Stidsholt, L., Greif, S., Goerlitz, H. R., Beedholm, K., Macaulay, J., Johnson, M., & Madsen, P. T. (2021). Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction. *Science Advances*, 7(10), eabf1367.
- Ten Cate, C., & Spierings, M. (2019). Rules, rhythm and grouping: Auditory pattern perception by birds. *Animal Behaviour*, 151, 249–257.
- Terhune, J. M. (2019). The underwater vocal complexity of seals (Phocidae) is not related to their phylogeny. *Canadian Journal of Zoology*, 97(3), 232–240. <https://doi.org/10.1139/cjz-2018-0190>
- Tønnesen, P., Oliveira, C., Johnson, M., & Madsen, P. T. (2020). The long-range echo scene of the sperm whale biosonar. *Biology Letters*, 16(8), 20200134. <https://doi.org/10.1098/rsbl.2020.0134>
- Verga, L., Sroka, M. G. U., Varola, M., Villanueva, S., & Ravignani, A. (2022). Spontaneous rhythm discrimination in a mammalian vocal learner. *Biology Letters*, 18(10), 20220316.
- Williams, H., & Staples, K. (1992). Syllable chunking in zebra finch (*Taeniopygia guttata*) song. *Journal of Comparative Psychology*, 106(3), 278–286. <https://doi.org/10.1037/0735-7036.106.3.278>
- Wund, M. A. (2006). Variation in the echolocation calls of little brown bats (*Myotis lucifugus*) in response to different habitats. *The American Midland Naturalist*, 156(1), 99–108.
- Yoshida, S., & Okanoya, K. (2005). Evolution of turn-taking: A bio-cognitive perspective. *Cognitive Studies: Bulletin of the Japanese Cognitive Science Society*, 12(3), 153–165.
- Zimmer, W. M. X., Madsen, P. T., Teloni, V., Johnson, M. P., & Tyack, P. L. (2005). Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. *The Journal of the Acoustical Society of America*, 118(5), 3337–3345.

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