

A guild classification system proposed for anuran advertisement calls

Mike Emmrich¹, Miguel Vences², Raffael Ernst³, Jörn Köhler⁴, Michael F. Barej¹, Frank Glaw⁵, Martin Jansen⁶, Mark-Oliver Rödel¹

¹ *Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstr. 43, 10115 Berlin, Germany*

² *Zoological Institute, Technische Universität Braunschweig, Mendelssohnstr. 4, 38106 Braunschweig, Germany*

³ *Museum für Tierkunde, Senckenberg Natural History Collections Dresden, A.B. Meyer Building, 01109 Dresden, Germany*

⁴ *Hessisches Landesmuseum Darmstadt, Friedensplatz 1, 64283 Darmstadt, Germany*

⁵ *Zoologische Staatssammlung München (ZSM-SNSB), Münchhausenstr. 21, 81247 München, Germany*

⁶ *Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt/Main, Germany*

<http://zoobank.org/F50B443E-265E-4C93-8B7D-55F793075C1F>

Corresponding author: Mark-Oliver Rödel (mo.roedel@mfn.berlin)

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Abstract

Zoologists have widely acknowledged the utility of classification systems for characterising variation in anuran egg and clutch types, tadpole morphotypes, embryonic and tadpole development, amplexus types and reproductive modes. These classification systems have facilitated unambiguous communication between researchers, often working in completely different fields (e.g. taxonomy, ecology, behaviour), as well as comparisons among studies. A syntactic system, classifying anuran call guilds, is so far lacking. Based on examination of the calls of 1253 anuran species we present a simple, easy to use dichotomous key and guild system for classifying anuran advertisement calls – the call type most frequently emitted by anurans and studied by researchers. The use of only three call elements, namely clearly-defined calls, notes, and pulses, plus presence or absence of frequency modulation, allows assigning all currently known anuran advertisement calls to one of eight distinct call guilds defined here. This novel toolkit will facilitate comparative studies across the many thousand anuran species, and may help to unravel drivers of anuran call evolution, and to identify ecological patterns at the level of acoustic communities.

Key Words

Amphibia, Anura, bioacoustics, call guilds

Introduction

Communication strategies are omnipresent across all forms of life, ranging from prokaryotes, to plants, fungi, and animals (Miller and Bassler 2001; Bradbury and Vehrencamp 2011). The reasons why organisms communicate with each other are, thus, manifold. Essential elements in all forms of communication are (1) a sender and a receiver, and (2) a signal of sufficient detectability and distinctiveness, so as to avoid loss of information or misinterpretation by the receiver (Torricelli et al. 1986; Lucass et al. 2016). Researchers from many disciplines have exploited communication signals to address behavioural,

or evolutionary research questions (Ord et al. 2013; Schiestl and Johnson 2013), and also used data from such signals in integrative taxonomic approaches to the study of various animal groups, including anuran amphibians (Padial et al. 2010; Köhler et al. 2017).

The form of communication most frequently used by anurans is acoustic (Gerhardt and Huber 2002; for an in-depth review see Köhler et al. 2017). This form of communication co-evolved presumably along with hearing, allowing for precise sender–receiver communication systems to evolve (e.g. Tembrock 1982; Ryan 2001; Desutter-Grandcolas 2002; Gerhardt and Huber 2002). Acoustic signals have the potential to cover a broad spatial range, to

be characterized by rapid signal transfer rates, and to convey directionality (i.e., the location of the sender may be identifiable to the receiver; Rothgänger and Rothgänger 2011). Acoustic signals are usually generated by oscillation of internal (birds, mammals, amphibians, fish), or external morphological structures (e.g. insects) (Gerhardt and Huber 2002; Bradbury and Vehrencamp 2011). These signals are mostly transmitted by air but also by using other material as carrier substrates (e.g. water or soil; Yager 1992; Platz 1993; Christensen-Dalsgaard and Elepfandt 1995; Seidel 1999; Lewis et al. 2001; Seidel et al. 2001; Bradbury and Vehrencamp 2011; Irisarri et al. 2011; Zheng et al. 2011). The main functions of intra-specific acoustic communication are attraction, detection and selection of mates, territoriality, and / or exchange of other information (e.g. warning or release; Bee and Gerhardt 2002; Ballentine et al. 2004; Wollenberg and Harvey 2010; Stephan and Zuberbühler 2014).

A considerable diversity of acoustic mating signals exists in anuran amphibians, and because they are the primary mate-recognition signals, they are usually species-specific (Ryan 2001; Gerhardt and Huber 2002; Köhler et al. 2017). Anuran call patterns are assumed to be largely genetically determined (Gerhardt et al. 1980; Duellman and Trueb 1994; Hödl 1996; Hoskin et al. 2005), with limited variation among individuals and populations (but see discussion of intra-specific call variation in Wells 2007 and Köhler et al. 2017). This particularly concerns the so-called advertisement calls, used (mainly) by males to advertise their location and to attract females (Mecham 1960; Zweifel 1968; Forester 1973; Ryan 2001; Gerhardt and Huber 2002; Wycherley et al. 2002; McLean et al. 2013).

In addition to understanding their function in mate attraction, taxonomists have made use of the species-specific and highly stereotyped nature of advertisement calls (Blair 1955, 1958; Littlejohn 1959; Schiøtz 1964, 1967, 1971, 1973), and of their simple characteristics, to identify and delimit frog species (see Köhler et al. 2017 for review). However, gaps in our understanding persist, and lead to questions over which factors drive the evolution of calls and trigger the differences in advertisement calls among species. Some properties of anuran advertisement calls are impacted by morphology. For example, frequency-related call characters usually correlate with body size (Ryan 2001; Gerhardt and Huber 2002). Although some call parameters can be modified by physiology (e.g., a frog's hormonal state; Wilczynski and Chu 2001), or temperature (Gerhardt 1978), the main bioacoustic characteristics of anuran calls are interpreted as fully heritable and only in exceptional cases shaped by learning (Dawson and Ryan 2009). From an evolutionary perspective, anuran advertisement calls are thus controlled by selection: sexual selection is most often discussed (Bradbury and Vehrencamp 2011), but an additional, less frequently-explored component is natural selection, due to the abiotic and biotic environment through which acoustic signals are transmitted (Marten and Maler 1977; Wiley and Richards 1978; Bullen and Fricke 1982; Forrest et al. 1992; Gerhardt and Huber 2002; Swearingen and White 2007; Bradbury and Vehrencamp 2011).

Anuran calls are structurally very variable (Heyer and Reid 2003; Köhler et al. 2017), leading to a broad range of definitions of call structures, complicating their comparability (Thompson et al. 1994; Gerhardt 1998; Ragge and Reynolds 1998; Gerhardt and Huber 2002; Köhler et al. 2017). A unified syntactic (i.e. structural) classification system, complementing available and widely applied semantic (i.e. functional) classification systems (compare Tembrock 1982; Gerhardt and Huber 2002) would therefore be desirable to facilitate communication among various sub-disciplines, eliminate imprecise terminology, and reduce ambiguity in interactions among researchers from different backgrounds or disciplines (Littlejohn 2001).

Semantic classification systems for anuran calls were proposed by Bogart (1960), Littlejohn (1977), and Wells (1977), and recently reviewed and updated by Toledo et al. (2015). On the other hand, Littlejohn (2001) suggested a syntactic classification. While semantic categorisations are needed to understand a species' behaviour and communication relative to conspecifics and the environment (Wells 1977; Toledo et al. 2015), the content of such information is not unique to a species. Syntactic classifications in contrast, focus on the structure of calls, and traditionally have been preferred by taxonomists (Thompson et al. 1994; Ragge and Reynolds 1998). A commonly used structural approach is guild classification. It can be particularly useful in understanding complex patterns in evolution and ecology (Wiens 1989; Williams and Hero 1998). Classifying advertisement calls into structural classes, or guilds, could, for instance, help to improve the understanding of complex interspecific soundscapes, or provide objective means of characterising acoustic partitioning of diverse species communities (Morton 1975; Hansen 1979; Rothstein and Fleischer 1987). The use of an objective, purely structural classification system could also allow for neutral baselines in the development of a hypothesis-driven framework to test predictions concerning natural *versus* sexual selection in call evolution. Herein, we follow a syntactic, guild-based approach in describing anuran advertisement calls. We follow the definition of advertisement calls by Toledo et al. (2015): a call produced in the "breeding season to attract mates and to segregate calling individuals". For other call types and their definitions see Wells (1977), Toledo et al. (2015) and Köhler et al. (2017). Our guild classification is based on the analysis of calls of 1253 anuran species from around the globe (Suppl. material 1: Table S1).

The aim of this paper is to propose a guild classification based on the acoustic properties of anuran advertisement calls. We do this by further developing the syntactic approach suggested by Littlejohn (2001). We focus on advertisement calls, because: (1) they are the most frequently used call type in taxonomic work, (2) they are the most commonly emitted call of frogs and therefore easy to collect and most accessible for analyses, and (3) they are species-specific because they are the primary mate-recognition signal in anuran amphibians. Thus advertisement calls should be under strong selection. A syntactic guild

classification for anuran advertisement calls should therefore facilitate addressing evolutionary and functional aspects in studies on amphibian biology and ecology.

Material and methods

Data collection

Herein, we aim to simplify and unify syntactic definitions of advertisement call characters in a way such that they can unambiguously be applied to mate-recognition acoustic signals of all anuran species. To establish an overview of advertisement call variability, we compiled and analysed advertisement calls from anuran species from around the globe. For these baseline data, we used call collections (Suppl. material 1: References), databases (Suppl. material 1: Web sources for calls used in this study), published call descriptions (Suppl. material 1: References), as well as our own call recordings of species from Africa, Madagascar and Guyana, in an attempt to cover a geographically and phylogenetically wide range of anuran diversity.

Because our primary goal was to include as much global frog diversity as possible, we did not apply any standardised search procedures (e.g., key word searches in Web of Science or Google Scholar), but simply accessed calls from freely available call collections, our own sound libraries, and published taxonomic papers. We used call descriptions that were published primarily after 1990, because earlier publications contained limited acoustic information, due to former technical limitations. To get comparable recordings, we re-sampled available recordings to uncompressed wav-format, with a sampling rate of 44.1 kHz. We used the software Soundruler 0.9.6 (Gridi-Papp 2007) to measure call variables and the software package Seewave (Sueur et al. 2008) for R to visualise waveforms and frequency spectra (R Core Team 2013). Oscillograms (waveforms) and audio spectrograms as well as results of the Fast Fourier Transformation (FFT; frequency spectrum) were examined for temporal and spectral characters, respectively (using 44.1 kHz sample ratio, 16 bits resolution, FFT window width = 256, window function = “Hanning”). The chosen FFT width represented the best compromise to achieve usable resolution and informative visualisation at both the temporal and spectral domain (Köhler et al. 2017). In cases where we had only published data available, but not the original recording, we incorporated the published data in our data set. Classifying a call as an advertisement call usually followed the original assignments of a call description by the respective authors, but we verified these assignments against the advertisement call definition by Toledo et al. (2015) before adding a call to our database (Suppl. material 1).

In total, we gathered published calls, call descriptions, or original recordings for 1426 species from 230 genera and 43 families. Anuran nomenclature and taxonomy were obtained directly from databases and publications (Frost 2019). For further background information and

best practices advice, concerning call recording, analyses, interpretation and presentation, see Köhler et al. (2017).

Definitions of anuran advertisement call units

For the purpose of developing a syntactic classification system of anuran advertisement call diversity, we established a globally applicable scheme that is as simple as possible but still sufficiently detailed to cover the currently known range of variation in these acoustic signals. To this aim, we surveyed advertisement calls of all included species, comprehensively, striving to identify distinct structural elements matching the criteria. We incorporated these elements into a dichotomous key, to allow for objective assignment of any species’ advertisement call to a distinct call guild. Following previous definitions of acoustic units of structural signal variation (Köhler et al. 2017), we identified three basic elements in common, apparently sufficient to comprehensively characterise acoustic signal variability: the call, notes, and pulses.

As the definitions of calls and call series is ambiguously dealt with in the literature (Köhler et al. 2017), it has previously been problematic to articulate an unequivocal, universal definition of an anuran “call”. However, such a definition is crucial, because a lack of consistency among disciplines and individual researchers in terminology related to a species’ call, a call series, and note, often hampers the interpretation and understanding of call descriptions. Previously such standardisations were largely ignored, resulting in idiosyncratic call descriptions that do not allow for comparative or meta-analyses. To minimise these problems, we followed and refined the note-centred approach suggested by Köhler et al. (2017) to define fundamental units of advertisement call variation.

*The term **call** is here used synonymous with advertisement call – the functional signal for mate-recognition, as the main acoustic unit in frog vocalisation. Calls are separated from other calls by silent inter-call intervals, typically longer (often several times longer) than the call itself. A **call series** is the temporal repetition of identical calls, repeated at rather regular intervals, and separated by larger gaps of silence from other call series (note that the definitions of our advertisement call guilds below do not take into account whether calls are arranged in series or not; only the call unit itself was considered). Under this definition, a call may be comprised of one or more subunits (Fig. 1b–e). These may differ in length and structure and are classified as either notes or pulses.*

*Calls are often sub-structured into two or more **notes**. Notes are subunits separated by intervals of silence (100% amplitude modulation), with the duration of these intervals being usually short relative to the duration of the note. Periods of silence are longer between notes than between pulses (see below) that form such notes (if pulsed), and shorter than the periods of silence between calls.*

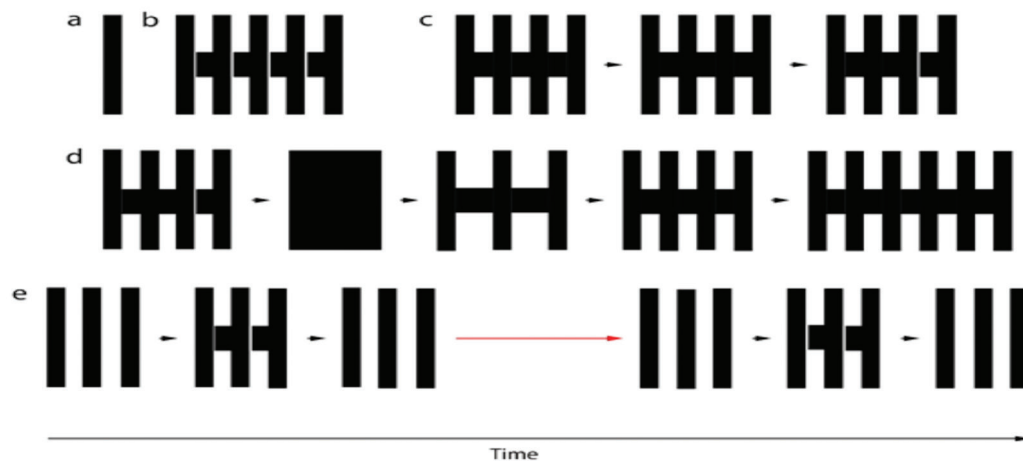


Figure 1. Basic types of anuran vocalizations based on their temporal structure, shown as schematic waveforms, modified after Littlejohn (2001): (a) non-pulsed call, (b) pulsed call, (c) call with uniform pulsed notes, (d) complex call containing different note types, and (e) two complex calls in a call series. Black arrows mark inter-note intervals and red arrow marks inter-call interval.

It must be mentioned that in a call consisting of only one unit (with or without subunits of the pulse category; Fig. 1a, b), the definition of a note and a call would apply simultaneously to the same, making them synonymous (Köhler et al. 2017). Because we follow this note-centred approach, we use the term call for the broader, encompassing unit. With this definition, it is only necessary to use all three terms if a call consists of at least three different units, separated by unequal periods of silence (Fig. 1c–e).

Notes sometimes contain a sub-structure produced by amplitude modulation within the note. These units are defined as pulses, following Köhler et al. (2017):

A pulse is the shortest, undividable unit in anuran vocalisation, with a typical duration of less than 50 ms.

In addition to these formalised syntactical advertisement call units, we included modulation of dominant spectral frequency. Frequency modulation can be depicted visually from spectrograms by a clearly visible increase or decrease in dominant frequency (“dfrq” in Hz). Modulation can be objectively quantified by subtracting the end-frequency from the start-frequency, and dividing this value by call duration (in ms). We calculated dominant frequency modulation (dfrq/ms) of all species with calls exhibiting frequency modulation, based on one representative call of the respective species. Values of $\geq 1/-1$ Hz/

ms were considered as a significant change in dominant frequency and all species were assigned to one of two binary character states, namely “not frequency modulated” ($< 1/-1$ Hz/ms) or “frequency modulated” ($> 1/-1$ Hz/ms).

After filtering our initial recordings representative of 1426 species and removing calls of insufficient quality (e.g. call descriptions lacking data for frequency modulation; visualisation only comprising either oscillogram or spectrogram; figures of insufficient quality; or recordings consisting of only one single call) from our dataset, we retained calls of 1253 species for final classification (Suppl. material 1: Table S1). We used these remaining calls to formalise the advertisement call structural (syntactic) guild classification presented in the following key.

Results

The combination of call units (call, note, and pulse) and frequency modulation allowed us to define eight distinct structural (syntactic) call guilds (Guilds A–H, Table 1). With a dichotomous key, the advertisement calls of each of the 1253 species could readily be assigned to one such guild. Below, we provide the guild classification key (Fig. 2), we summarise call guilds, and provide illustrative examples (respective spectrograms and waveforms, plus species identifications in Fig. 3.)

Key to anuran Advertisement Call Guilds

(compare Fig. 2 and descriptions below)

1	call consists of only one acoustic unit	2
1'	call contains several acoustic units	3
2	dominant frequency without significant change over call duration.....	
 Call Guild A: “non-frequency modulated, non-pulsed simple call”	
2'	dominant frequency with significant change over call duration	
 Call Guild B: “frequency modulated, non-pulsed simple call”	

3 call comprises pulses but no notes 4
 3' call comprises several pulsed notes 5
 4 dominant frequency without significant change over call duration: Call Guild C: “non-frequency modulated pulsed call”
 4' dominant frequency with significant change over call duration: Call Guild D: “frequency modulated pulsed call”
 5 call comprises several structurally (more or less) similar notes 6
 5' call comprises structurally distinctly different notes 7
 6 dominant frequency without significant change over call duration
 Call Guild E: “non-frequency modulated call with uniform notes”
 6' dominant frequency with significant change over call duration
 Call Guild F: “frequency modulated call with uniform notes”
 7 dominant frequency without significant change over call duration
 Call Guild G: “non-frequency modulated complex call”
 7' dominant frequency with significant change over call duration in at least one of the distinct note types
 Call Guild H: “frequency modulated complex call”

Short description of call guilds with species examples

Here we summarise the “diagnostic” characters of the different call guilds, give some species examples for each guild and refer to respective illustrations of selected exemplary calls (Fig. 3). The sources for the specific examples are summarised in Suppl. material 1: Table S1.

Call Guild A “non-frequency modulated, non-pulsed simple call”: call consists of one single continuous signal (which can be of any duration) with no significant change in dominant frequency. Examples: *Alytes cisternasii* (Alytidae), *Bombina bombina* (Bombinatoridae), *Eleutherodactylus tonyi* (Eleutherodactylidae), *Heleophryne depressa* (Heleophrynidae), *Rana arvalis* (Ranidae).

Call Guild B “frequency modulated, non-pulsed simple call”: call consists of one single continuous signal

(which can be of any duration) with a significant change in dominant frequency. Examples: *Rhaebo haematiticus* (Bufonidae), *Pristimantis bambu* (Craugastoridae), *Ameerega pepperi* (Dendrobatidae), *Kassina senegalensis* (Hyperoliidae), *Leptodactylus fuscus* (Leptodactylidae), *Limnodynastes peronii* (Limnodynastidae), *Austrochaperina fryi* (Microhylidae), *Strongylopus grayii* (Pyxicephalidae), *Chiromantis vittiger* (Rhacophoridae).

Call Guild C “non-frequency modulated, pulsed call”: call comprised of several similar, but distinguishable acoustic signals (pulses). Pulses are arranged in a single group (note = call), meaning that intervals between pulses are equally long, but much shorter than inter-call intervals. The dominant frequency does not change over the call duration. Examples: *Dendropsophus tritaeniatus* (Hylidae), *Eleutherodactylus toa* (Eleutherodactylidae), *Hemismus marmoratus* (Hemisotidae), *Cophixalus concinnus* (Microhylidae).

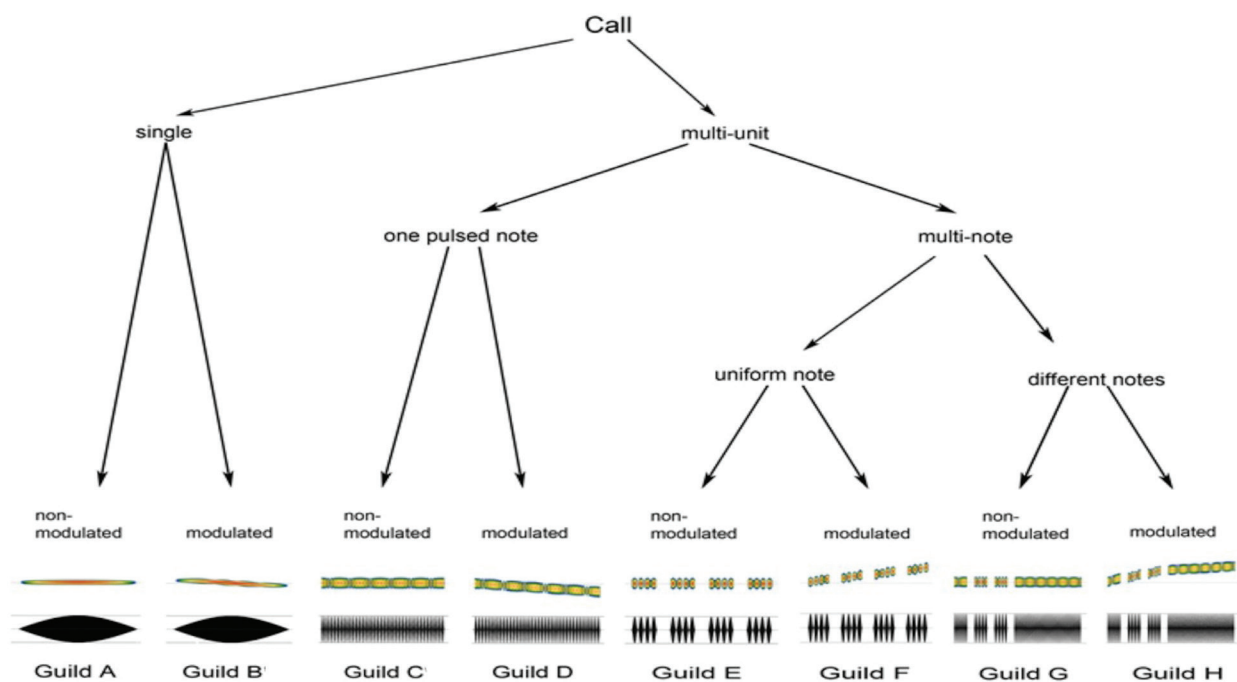


Figure 2. Key to anuran advertisement call guilds (compare text); each guild illustrated by schematic waveform and spectrogram.

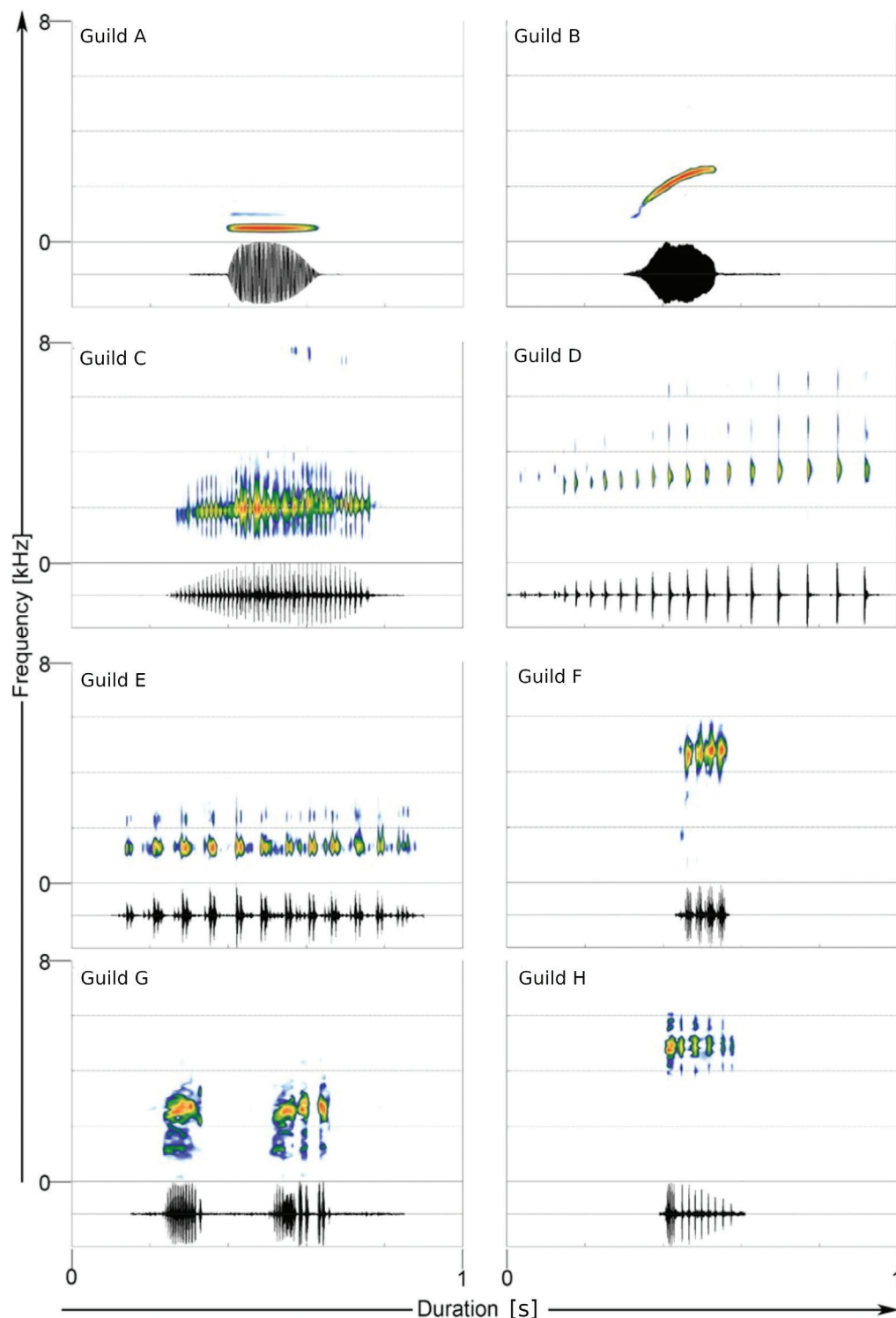


Figure 3. Examples for all different anuran advertisement call guilds (A–H), with a time scale of 0 to 1 s on x-axis and frequency scale of 0 to 8 kHz on y-axis (compare text). Guild A) non-frequency modulated, non-pulsed simple call (*Bombina bombina*; Bombinatoridae; $dfrq/ms = 0.00$ Hz/ms) (based on Schneider 2005); Guild B) frequency modulated, non-pulsed simple call (*Leptodactylus fuscus*; Leptodactylidae; $dfrq/ms = 7.22$ Hz/ms) (based on Márquez et al. 2002); Guild C) non-frequency modulated pulsed call (*Hyla meridionalis*; Hylidae; $dfrq/ms = 0.67$ Hz/ms) (based on Masó and Pijoan 2011); Guild D) frequency modulated pulsed call (*Hyperolius pickersgilli*; Hyperoliidae; $dfrq/m = 2.32$ Hz/ms) (based on Du Preez and Carruthers 2009); Guild E) non-frequency modulated call with uniform notes (*Sclerophrys mauritanica*; Bufonidae; $dfrq/ms = 0.31$ Hz/ms) (based on Masó and Pijoan 2011); Guild F) frequency modulated call, with uniform notes (*Pseudopaludicola boliviana*; Leptodactylidae; $dfrq/ms = 2.38$ Hz/ms) (based on Márquez et al. 2002); Guild G) non-frequency modulated complex call (*Smilisca sila*; Hylidae; $dfrq/m = 0.43$ Hz/ms) (based on Ibanéz 1999); Guild H) frequency modulated complex call (*Hyperolius nasutus*; Hyperoliidae; $dfrq/ms = 1.66$ Hz/ms) (based on Du Preez and Carruthers 2009).

Table 1. Number of species studied (N = 1253) per call guild; for guild definitions compare text and Fig. 2.

	N	Percentage
Guild A	130	10.4%
Guild B	198	15.8%
Guild C	454	36.3%
Guild D	247	19.7%
Guild E	81	6.5%
Guild F	22	1.8%
Guild G	93	7.4%
Guild H	28	2.3%
Total	1253	100.0%

Call Guild D: “frequency modulated, pulsed call”: call comprised of several similarly structured, but distinguishable acoustic signals (pulses). Pulses are arranged in a single group meaning that intervals between pulses are equally long, but much shorter than inter-call intervals. The dominant frequency changes significantly over the call duration. Examples: *Pristimantis w-nigrum* (Craugastoridae), *Acris gryllus* (Hylidae), *Diasporus vocator* (Eleutherodactylidae), *Mantidactylus tricinctus* (Mantellidae), *Agalychnis callidryas* (Phyllomedusidae), *Ptychadena taenioscelis* (Ptychadenidae), *Rana muscosa* (Ranidae), *Kurixalus appendiculatus* (Rhacophoridae).

Call Guild E “non-frequency modulated call with uniform notes”: call comprised of several similarly structured notes. Dominant frequency does not change over the call duration. Examples: *Boana leptolineata* (Hylidae), *Blommersia grandisonae* (Mantellidae), *Leptobranchium leucops* (Megophryidae), *Oreophryne clamata* (Microhylidae), *Mixophyes fleayi* (Myobatrachidae), *Lithobates virgatipes* (Ranidae).

Call Guild F “frequency modulated call with uniform notes”: call comprised of several distinguishable notes. These notes are structurally very similar to each other. Dominant frequency changes significantly over the call duration. Examples: *Boana almendarizae*, *Osteocephalus yasuni*, *Scinax nebulosus* (Hylidae), *Pseudopaludicola boliviana* (Leptodactylidae), *Ptychadena schillukorum* (Ptychadenidae).

Call Guild G “non-frequency modulated, complex call”: call comprised of several notes. The signals are arranged in several, at least two, structurally different note types. Dominant frequency does not change over the call duration. Examples: *Melanophryniscus atroluteus* (Bufonidae), *Hyperolius benguellensis* (Hyperoliidae), *Boophis bottae* (Mantellidae), *Litoria fallax* (Pelodryadidae).

Call Guild H “frequency modulated, complex call”: call comprised of several notes, at least two being structurally different. Dominant frequency changes significantly over the call duration in at least one of the distinct note types, e.g. *Smilisca sila* (Hylidae), *Cochranella granulosa* (Centrolenidae), *Engystomops pustulosus* (Leptodactylidae).

Discussion

Syntactic classification systems allow for unambiguous communication between researchers and comparisons be-

tween studies. For instance, the frequent adoption, application, and widespread use of clear definitions of anuran egg types, tadpole morphotypes, and developmental stages (Gosner 1960; Altig and Johnston 1989; Altig and McDiarmid 2007; Schulze et al. 2015), anuran reproduction modes (Duellman and Trueb 1994; Haddad and Prado 2005), modes of amplexus (Carvajal-Casto et al. 2020), and anuran call types (Wells 1977; Toledo et al. 2015), have demonstrated their substantial value for herpetologists.

In this paper, we present a simplified guild classification system for anuran advertisement calls. In order to avoid assignment of individuals from one species to different guilds, we have not included body size-driven traits like dominant frequency, temperature-driven traits like pulse rate, or motivation-driven traits like inter-call interval duration or call rate. The use of only three call elements (call, note, pulse, plus the presence or absence of frequency modulation), allows for the unambiguous allocation of any anuran advertisement call currently known to us to a distinct syntactic, non-functional, call guild.

The number of species investigated by us, although covering the majority of families, habitats and regions, represents only a small proportion (about 17%) of the currently known anuran species (> 7100; Frost 2019; last accessed 10 March 2020). It is thus possible, or even likely, that advertisement calls discovered in the future may not perfectly fit our proposed guild system. However, this system could easily be extended. For example, the proposed guilds could be divided by differentiating within a guild the maximum of amplitude (initial, centred or terminal of call), the dominant frequency (low, medium or high-pitched calls), the direction of frequency modulation (negative or positive), or by the distinction between pulsatile and tonal calls.

Our definition of call guilds may not only allow for better comparisons between variable call descriptions, as suggested by Krause (1987), but a syntactic classification based on acoustics may also enable improved insight into the life-history of species. Most anurans behaviourally select and call from species-specific breeding sites (Duellman and Trueb 1994; Wells 2007). Different calling behaviour and different habitats both affect signal propagation through call-specific environments in different ways. Abiotic (e.g., humidity or air pressure) and biotic factors (e.g., vegetation density or structure) may affect sound waves (Bradbury and Vehrencamp 2011). Propagation properties may change due to an individual (usually male) frog, calling from different substrates or microhabitats, such as trees, leaf-litter, from water, underground, or, if they call singly or in a chorus (Lopez et al. 1988; Forrest 1994; Lardner and bin Lakim 2002). Intrinsic factors such as body condition or fatigue can also change propagation properties (Humfeld 2013; Jansen et al. 2016). Call properties and calling behaviour, thus, may be adjusted behaviourally to avoid or reduce information loss or alteration of structure. Many breeding sites share similar features, such as stagnant versus flowing streams, open or closed vegetation (Hödl 1977; Kwet 2001;

Schlüter 2005), and characteristics of such microhabitats may alter sound in specific ways. For instance, torrent water introduces background noise, which may simply mask the call (or certain frequency components); dense vegetation may cause scattering, blurring, or reflections, particularly of amplitude-modulated calls (Bradbury and Vehrencamp 2011). Thus, habitat characteristics may force or select for species living in similar environments to share specific combinations of call elements. It is possible that the call guild types presented herein are coupled to certain behavioural patterns and thus allow predictions about the behaviour of species. Several correlations between bioacoustics and habitat, behaviour, or morphology have already become known in frogs, as well as in other animals (Etges 1987; Krause 1987; Hödl 1996; Martins et al. 2006; Vasconcelos and Rossa-Feres 2008; Both and Grand 2012; Sinsch et al. 2012). For example, Neotropical birds living in dense understorey show less frequency modulations than birds of more open habitats (Morton 1975). However, it is unlikely that call properties are determined by single factors; acoustic signals will be, apart from phylogeny, shaped by various environmental and species-specific characters (Goutte et al. 2018).

By classifying calls according to structural elements, our syntactic call guilds might assist in detecting such general correlations between call characteristics and natural history, or habitat. Based on the calls of the 1253 species considered in this study, the most common call guilds were guilds C and D, followed by guilds A and B (Table 1). Calls with more complex structures, like guilds E to H, were less frequent. Frequency modulation was most often associated with simple and relatively short calls, whereas complex calls were less likely to consist of frequency modulated elements.

Our guild system is not suited to discriminate between closely related species or to describe species; it is, thus, not a tool for taxonomy. However, it might be used as a first “sorting step” for an acoustic characterisation in call descriptions, and it may help to facilitate the understanding of anuran advertisement call evolution. For example, a semantic classification of advertisement calls assumes that similar calls comprise the same information (Wells 1977; Toledo et al. 2015). However, the informational content of advertisement calls often differs (Ryan 2001; Gerhardt and Huber 2002). An increase in call complexity may be related to more, or different, social interactions, like in *Engystomops pustulosus* (Ryan et al. 1982; Ryan 1985; Ryan and Rand 1990; Baugh and Ryan 2010). The ultimate adaptive significance for such reduction or addition of information may be indicative of interactions of species with their abiotic and biotic environments. The simple classification of call guilds based on structure may facilitate interpretation of these acoustic interactions and help clarify the origin of call components or structures. Finally, we envision that our syntactic call guide classification scheme will be a useful tool set for future meta-analyses and comparative studies concerning the evolution of anuran acoustic signals. However, inclusion of

questions relating to how the environment, morphology, life-history and phylogeny shape anuran advertisement calls, remains a challenge for forthcoming studies.

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Supplementary material 1

Database for the definition of anuran call guilds

Authors: Mike Emmrich, Miguel Vences, Raffael Ernst, Jörn Köhler, Michael F. Barej, Frank Glaw, Martin Jansen, Mark-Oliver Rödel

Data type: DOCX file

Explanation note: **Table S1:** List of 1253 anuran species with advertisement calls; **References** (literature and CDs) for anuran calls used in this study; **Web sources** for anuran calls used in this study.

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Autor(en)/Author(s): Emmrich Mike, Vences Miguel, Ernst Raffael, Köhler Jörn, Barej Michael F., Glaw Frank, Jansen Martin, Rödel Mark-Oliver

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