



## SONGS AND CALLS: PERSPECTIVES ON CREATING A GLOBAL DEFINITION

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**Abstract** · Historically, bird vocalizations have been split into two main categories: calls and songs. This categorization has been based mainly on the duration and complexity of the vocalization, although other criteria including function, development, and phylogeny have been included to separate both vocalizations. Over the last decade, an increasing number of studies examining the structure, function, and evolution of vocalizations, especially for species that breed in the tropics, have revealed that the current definitions of songs and calls no longer match our current knowledge of bird vocalizations. Here, we propose a new global definition of calls and songs that matches our current knowledge of this topic. Additionally, we review several key assumptions that have been used to classify songs and by association calls, and we present clear examples that contradict these previous assumptions, thereby limiting the definition of songs and calls. Our proposed call and song definitions correct the ambiguity of previous definitions that use complexity and duration, or omit vocalization functions, and reflect the diverse and multifunctional properties of avian vocalizations.

### Resumen · Cantos y llamadas: perspectivas para crear una definición global

Históricamente, las vocalizaciones de las aves se han dividido en dos categorías principales: llamadas y cantos. Esta categorización se ha basado principalmente en la duración y la complejidad de la vocalización. Aunque otras definiciones incluyen criterios adicionales como la función, el desarrollo y la filogenia para diferenciarlas. En la última década, el creciente número de estudios sobre la estructura, función y evolución de las vocalizaciones, especialmente para las especies que se reproducen en los trópicos, ha revelado que las definiciones actuales de cantos y llamadas ya no coinciden con el conocimiento actual de las vocalizaciones de aves. Aquí proponemos una nueva definición global para llamadas y cantos que coincide con el conocimiento actual sobre este tema. Además, revisamos varios supuestos clave que se han utilizado para clasificar cantos y, por ende, llamadas, y presentamos ejemplos claros que contradicen los supuestos anteriores y que por lo tanto, limitan la definición de cantos y llamadas. Las definiciones que proponemos corrigen la ambigüedad de las anteriores, que utilizan la complejidad y la duración, o que omiten las funciones de las vocalizaciones. Con esto pretendemos aportar definiciones más amplias, que se ajusten a los últimos avances en el campo de la comunicación de las aves, y que demuestran que los cantos y las llamadas son más diversas y complejas de lo que se pensaba anteriormente.

**Key words:** *acoustic communication · bioacoustics · call definition · song definition · vocalizations*

Bird vocalizations are structurally diverse and multifaceted, and vary individually, geographically, and among sexes and species (Falls 1982, Nelson 1989, Seddon 2005, Podos & Warren 2007). Historically, bird vocalizations have been split into two main categories: songs and calls. The distinction between these categories has been primarily based on the duration and complexity of the vocalization, although other criteria, including function, development, and phylogeny, have been considered (Spector 1994, Marler 2004, Catchpole & Slater 2008). At the time of his review of birdsong definitions, Spector (1994) noted that “song concepts have and will continue to change over time.” Given the recent developments in our comprehension of bird vocalizations, the need to refine these definitions has become apparent because they no longer match our current knowledge of bird vocalizations (Price 2015).

Before we discuss further alterations in vocalization definitions, it is important to reflect on several past and current definitions. For example, Andersson (1994) described songs as “long-range acoustic signals produced mainly during the breeding season” and further stated that “song is often conspicuous and frequent”. Along with these features, Andersson (1994) described song as a sexually selected trait that confers a competitive advantage over rivals of the same sex when competing for reproductive opportunities with the opposite sex. By comparison Catchpole and Slater (2008) defined songs as “generally long complex vocalizations produced by males during the breeding season,” although they noted that there are many exceptions that do not necessarily fit this definition. More recently, Bonnevie & Craig (2018) defined song as a “sequence of several vocal elements with species-specific characteristics, performed with a particular rhythmic pattern, which serves for intraspecific communication in birds”. With respect to calls, their definition is often rooted in and related to the definitions of bird song. Generally, calls are described as short simple vocalizations used to initiate and maintain contact between birds or to alarm individuals of potential threats (e.g., Marler 2004, Catchpole & Slater 2008). Combined, these definitions have been developed to account for the variation observed in the songs and calls of birds and to allow for comparisons of acoustic signals across species.

In this commentary, we examine several key assumptions used to classify songs and by association calls. We also present several examples that contradict these previous assumptions, thereby potentially limiting the previous and present theories used to define

Submitted 29 Feb 2020 · First decision 12 Mar 2020 · Acceptance 20 Jun 2024 · Online publication 6 Jan 2025

Communicated by Paulo C. Pulgarín R.

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songs. In addition, we propose several key elements that we consider important when building a global definition of songs and calls, and we use these elements to create a new definition for these two categories of bird vocalizations. The purpose of this commentary is to continue the discussion of the characteristic features of songs and calls. With the advancement in recording equipment and the accumulation of such large avian vocalization datasets, it remains important to continue this discussion to increase our comprehension of the diversity, function, and variation observed in the field of avian bioacoustics.

When reviewing these previous definitions, we note several key assumptions about songs and calls: 1) songs are produced by males, 2) songs are produced during the breeding season, 3) songs are used for intraspecific communication, and 4) songs are longer and more complex, whereas calls are short and simple. Historically, the definitions of songs and calls were primarily conceived to define the songs of species living at northern latitudes in temperate zones (Marler 2004, Catchpole & Slater 2008). Therefore, it is no surprise that these definitions work especially well for the majority of species that breed in temperate zones (Catchpole & Slater 2008). In temperate regions, males are the primary singing sex, and songs are produced mostly during the breeding season for mate attraction and male-male interactions (Gil & Gahr 2002, Collins 2004). Finally, it should come as no surprise that songs are viewed as having greater complexity and duration than calls, because of the large amount of literature that has focused on the influence of sexual selection in the design of these acoustic signals (reviewed by: Andersson 1994, Collins 2004, Catchpole & Slater 2008). Given the key role that songs play in mate attraction, they are likely to become more complex and exaggerated than calls produced by birds if they are acted upon by sexual selection (Catchpole 1980, Collins 2004).

Although songs have been viewed primarily as a male trait, both males and females in many tropical species produce songs (Slater & Mann 2004). Furthermore, a recent study found that female song is more common and widespread than previously thought and is the ancestral trait in songbirds (Odom et al. 2014). In addition, recent studies have found that, for some species, including African Black Coucals *Centropus grillii*, Streak-backed Orioles *Icterus pustulatus*, and Stripe-headed Sparrows *Peucaea ruficauda*, vocal output is greater in females than in males (Price et al. 2008, Geberzahn et al. 2009, Illes 2015). These examples demonstrate that songs must be viewed as acoustic signals produced by both males and females when constructing a global definition. These findings are especially interesting from the perspective of Andersson's (1994) definition of song as a sexually selected trait because previous investigations have focused exclusively on female selection; however, some consideration must be given to potential male selection in the evolution of female songs. This area offers an exciting field of research and may provide significant insight into the evolution of acoustic signals.

The second assumption focuses on the exclusive use of songs during the breeding season. Again, examples from studies of tropical species show that songs are used outside the breeding season because they play a critical role in year-round territory defense (Tobias et al. 2011, Illes 2015). Many research disciplines have stressed the importance of studying the full annual cycle of birds (Marra et al. 2015) and studying acoustic signals outside the breeding season may offer new perspectives on avian vocalization functions.

The third assumption focuses on the use of songs and calls for intraspecific communication. Many previous definitions do not explicitly state that songs cannot be used for interspecific communication, except for the definition proposed by Bonnevie & Craig (2018). Although songs and calls may be used more often for intraspecific communication, there are many examples of interspecific communication where one species attempts to exclude other species from areas through competitive interactions

or where they use acoustic signals to attract other species. For example, Swamp Sparrows *Melospiza georgiana* compete with Song Sparrows *M. melodia* for habitat, and use songs to deter competitors during interspecific interactions (Peters et al. 1980). Similarly, males of Peruvian Warbling-Antbird *Hypocnemis peruviana* and Yellow-breasted Warbling-Antbird *H. subflava* exhibit the same territorial behavior towards the songs of both intraspecific and interspecific competitors (Tobias & Seddon 2009). Calls are also used for a combination of intraspecific and interspecific communication. For example, in Paridae, species calls encode information for signaler identity and group affiliation, which is used for intraspecific communication, but also encode information about resource discovery and predator threat to which both intraspecific and interspecific individuals respond (Hurd 1996, Mahurin & Freeberg 2008, Wilson & Mennill 2011), including species that have never heard these calls before (Nocera et al. 2008, Sandoval & Wilson 2022). Another example of the dual function of calls is the chip call of White-eared Ground-Sparrows *Melospiza leucotis*. Intraspecific individuals exclusively respond at low call rates (<32 calls per minute) because they act as a contact signal. At high call rates (i.e., 60 or 84 calls per minute), however, both intraspecific and interspecific individuals respond because the vocalization is used as an alarm call against predators (Méndez & Sandoval 2017). These examples demonstrate the limits of defining songs as vocalizations used only for intraspecific communication, and calls as vocalizations used for both intra and interspecific communication. Both songs and calls are multifaceted and are employed in various contexts with intraspecific and interspecific individuals. Any definition that does not include each vocalization's function(s) will confound our ability to produce solid global song and call definitions.

Finally, the structure and design of the signal has played a key role in the categorization of songs and calls. Catchpole & Slater (2008) noted that calls are shorter and simpler than songs and are produced by both sexes year-round. Recent studies have demonstrated that assumptions about the structure and design of avian vocalizations may need to be reconsidered. For example, species such as the Great Curassow *Crax rubra* and Corn Crake *Crex crex* produce vocalizations with spectrotemporal characteristics that are traditionally classified as calls, even though these vocalizations are used in a function similar to that of songbirds' songs (i.e., vocalizations are used to attract mates and defend territories; Baldo & Mennill 2011, Budka & Osiejuk 2017). We often associate songs specifically with oscine passerines, and for this reason, the vocalizations of non-passerines like the Great Curassow or the Corn Crake may have been overlooked as songs. Although oscine passerines are known to produce long, complex songs, there are examples of oscine passerines that produce short and simple songs in comparison to calls, including Black-capped Chickadee *Parus atricapillus* and House Sparrow *Passer domesticus* (Ficken et al. 1978, Charrier et al. 2004, Anderson 2006). These examples demonstrate that complexity may not be a discerning trait enough to distinguish and categorize songs and calls. At first, this movement away from using spatiotemporal structure to define songs may seem problematic, but it reinforces the importance of incorporating and using other characteristics to create a global definition for songs and calls.

With all of the new information that is being collected about bird vocalizations, creating a new definition of bird songs and calls that can be applied to the vocalizations of birds across the globe is a somewhat daunting task. This endeavor is especially important given that the majority of bird species are found in the tropics (approximately 8000 species; Stutchbury & Morton 2001), and historical and current definitions do not adequately apply to the ample vocal behavior of bird species. Therefore, we suggest and encourage that any new song and call meanings should include function as a describing feature, as we propose in the following definitions:

**Song.** A sequence of vocal elements produced by adult males or females in species with or without a syrinx used for short- or long-range communication to attract and defend mates (e.g., duetting for pair contact), intra- and intersexual interactions (e.g., territory defense or mate guarding), and to defend resources (e.g., non-breeding territories, food, singing perches, or roosting sites).

**Call.** Vocal elements produced by adult and juvenile males and females in species with or without syringes used only for short-range communication to transmit information unrelated to mating, intrasexual interactions, or defending resources.

These definitions aim to build on previous ones that use complexity, duration, or omit vocalization functions (Andersson 1994, Marler 2004, Catchpole & Slater 2008, Bonnevie & Craig 2018). We attempted to create a definition that moves past previous assumptions. Our song definition attempts to include soft songs (short-range communication) along with regular amplitude songs (long-range communication). In the case of soft songs, the nature of the communication requires secrecy, so individuals reduce song amplitude because the intended receiver is in close proximity, and the message and interaction need to be encrypted (McGregor & Dabelsteen 1996, Vargas-Castro et al. 2017). This example further emphasizes the importance of function for the vocalization, and the necessity of incorporating function into all future definitions of songs.

In conclusion, these examples represent only a small portion of the complex and diverse vocalizations produced by birds. Furthermore, the advancement of knowledge in the field of avian communication continues to show that songs and calls are more diverse and multifunctional than previously thought. Therefore, it is necessary to revisit previous assumptions and adjust current definitions to pair with this new knowledge, especially for comparative studies looking to understand song function across broad groups of species in different taxonomic groups.

## ACKNOWLEDGEMENTS

We thank David Wilson, Alana Demko, Gilbert Barantes, and two anonymous reviewers for all comments on an early draft that improve this comment. LS was supported by Vicerrectoría de Investigación, Universidad de Costa Rica under grant numbers C2705 and C3025.

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