# Salientia Communication

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## Introduction

Animal communication occurs when a sender exchanges information, through a codified signal, with a receiver to the benefit of both. In anurans, communication is notorious during courtship and male-male agonistic interactions. Usually, males advertise their presence and readiness to mate while keeping rival males at bay, whereas females scrutinize chants in order to assess males' qualities and choose preferable partners (see Vallejos et al. 2017 for an exception). Thus, in most species, signals are primarily produced by males, placing them as senders and receivers, while females act mainly as receivers (Gerhardt and Huber 2002). In this section, we synthesize studies on anuran senders and receivers, what sort of information they exchange, what are the signals, and how they are produced and transmitted in anuran interactions. Moreover, we examine potential communication modalities based on observed sensory cues perception by conspecifics.

Because anurans communicate primarily via acoustic signals, other sensory modalities seem to have been neglected for a long time and have only recently received more attention (Starnberger et al. 2014a, b; Woodley 2015). Recent studies have reported alternative modalities such as chemical and tactile communication. Additionally, for most vertebrate groups, communication has been shown to occur through complex signaling, composed of multi-sensory modalities. These signals are frequently referred to as "multimodal." Possible causes and functions of multimodal signaling in anurans are based on behavioral field observations and experimental tests.

## Acoustic Communication

Calling activity is the primary communication mechanism for anuran amphibians (Gerhardt and Huber 2002). Each anuran species can have distinct vocalization patterns, and individual frogs produce a variety of calls, for which several distinct categories are recognized (Toledo et al. 2015). Several authors have proposed classifications and categories for the calls emitted by

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anurans (e.g., Duellman and Trueb 1994; Wells 2007). Recently, Toledo et al. (2015) standardized the anuran call classification, with 13 distinct call types, which can be divided into 3 categories according to social context: (1) reproductive, (2) aggressive, and (3) defensive.

Reproductive calls are the most commonly heard and with the highest value for systematics due to its function as an important premating isolation mechanism. Advertisement calls are long-range signals emitted usually by males during breeding season to attract conspecific females for reproduction. A single male's call usually reveals its species, sex, reproductive state, and location. This call can also attract males at a long distance to join the chorus and might be used to establish territorial limits for conspecifics (Toledo et al. 2015; Köhler et al. 2017). More than five types of reproductive calls have been proposed for anurans: courtship, amplectant, release, post-oviposition male release, and rain calls (see Toledo et al. 2015 for further definitions).

Aggressive calls are emitted by male frogs to defend their calling sites against conspecific competitors. Territorial call, the most common of this category, is emitted by males defending specific resources inside a territory like the calling, egg laying, retreat, or feeding sites. Consequently, this call acts by setting boundaries between males in a reproductive chorus. There are another three types of aggressive calls described for anuran species: encounter, fighting, and displacement (see Toledo et al. 2015 for further definitions). Besides the aforementioned categories, three subcategories (alarm, distress, and warning calls) of defensive calls are interpreted as adaptations to prevent predation (see Toledo et al. 2015 for further definitions).

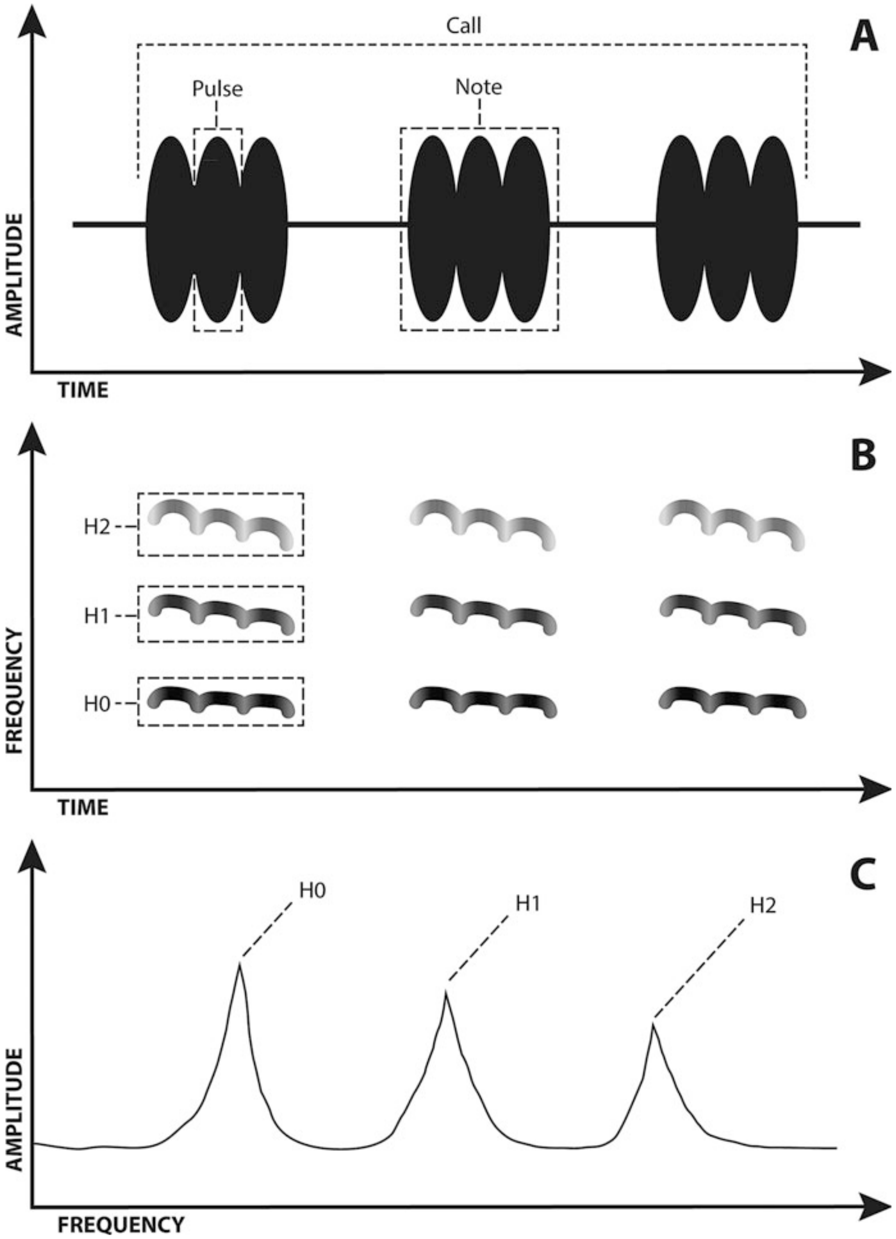
## Structures of Bioacoustic Signals

Sound is a pattern of transmitted energy through pressure waves. Wave components can be depicted in sound graphs, illustrating changes in amplitude over time (oscillogram) or transformed into frequency domains through a fast Fourier transformation, which decomposes the complex waveform into sine waves for analysis, producing spectrograms and power spectra (Fig. 1). Many sounds concentrate energy in several separate, evenly spaced frequency bands, called harmonics, which are multiples of the lowest harmonic (i.e., first or fundamental; see Fig. 1). The dominant frequency is the one that contains the greatest amount of energy. This can be either the fundamental frequency or one of its harmonics (Ryan 2001; Vitt and Caldwell 2013; Köhler et al. 2017).

Bioacoustic signals are divided into units (call) and subunits (notes and pulses). The term pulse applies to short signals, with a single unbroken wave train delimited in time by significant amplitude reduction. Notes are usually groups of pulses and the main subunit of a call, with short intervals, relative to total call length, of 100% amplitude modulation (i.e., silence) between them. Calls are the primary structure of an anuran acoustic signal and are separated from other calls by periods of silence (typically much longer than the call). Calls may be composed of one or several notes of the same type (simple call) or different types (complex call) (Köhler et al. 2017). The waveform shape of a call, note, or pulse is called envelope. A period is the duration of a call structure, unit or subunit, plus the interval between consecutive structures. Repetition rates are the number of such call structures emitted per period of time, usually per one second or minute (Ryan 2001; Köhler et al. 2017).

## Mechanisms of Sound Production and Reception

The basic mechanism of sound production in most anurans is activated while exhaling. A positive pressure, created by the contraction of muscles in the buccal cavity, pumps air into the lungs. Then, contraction of trunk muscles forces the air from the lungs into the buccal cavity, through the larynx, where it causes the vocal cords to vibrate and produce sounds. These sounds are further modified by muscles of the larynx and associated cartilages, between the



**Salientia Communication, Fig. 1** Oscillogram (**a**), spectrogram (**b**), and power spectrum (**c**) of a single hypothetical call composed of three notes with three pulses each. Note the first three harmonics indicated in **b** and **c**. The fundamental frequency (lowest band in **b**) corresponds to the dominant frequency (highest peak in **c**)

lungs and the buccal cavity. Then, such morphological structures are more developed in males. Exceptions to this sound production process can be seen in *Bombina* (during inspiration) and in *Discoglossus* (during both inspiration and expiration) (Wells 2007).

The anuran laryngeal apparatus lies between the lungs and the buccal cavity and therefore is involved in both respiration and sound production. In most anurans, the larynx is composed of a pair of arytenoid cartilages, which houses the vocal cords. These moveable cartilages are supported by the cricoid cartilage, which attaches the larynx to the hyoid apparatus and serves as a point of attachment for various muscles. The vocal cords can only be stimulated when the arytenoid cartilages are apart, allowing air flow through the larynx. In the family Pipidae, however, males lack vocal cords and use a modified laryngeal skeleton to produce sound. Calls consist of sharp clicking sounds produced when the arytenoid cartilages are suddenly pulled apart. Sounds are amplified by an enormous boxlike cricoid cartilage. Hence, sound production in pipids requires contraction of the laryngeal muscles, but does not involve contraction of the trunk muscles or the production of vibrations in an air stream (Duellman and Trueb 1994; Wells 2007).

In males of many frog species, vocal sacs are connected to the buccal cavity, typically via slit-like openings, and are inflated during vocalization. The vocal sac is not an acoustic cavity resonator as it was previously suggested, although it may serve to direct the call toward the receiver or as a reservoir of mechanical energy during calling. Morphology varies from a median single subgular sac to bilobate and paired subgular sacs or paired lateral sacs. Anuran vocal sacs can be slightly or highly distensible and are defined as either internal or external vocal sacs. Their form and color might also have a role in visual signaling (Wells 2007; Köhler et al. 2017).

Anurans have a large tympanic membrane of thin, nonglandular skin, which receives airborne sound waves and transfers sound pressure-induced vibrations to the columella in the middle ear. These vibrations disturb the fluids in the inner ear through the oval window between the columella and the inner ear. Within the anuran inner ear, two sensory organs are largely responsible for the perception of airborne sounds: the amphibian papilla, sensitive to low and mid-frequencies (typically 50 Hz to 1 kHz), and the basilar papilla, sensitive to higher frequencies (above 1 kHz). Some anurans species, however, lack tympanic membranes, columella, or even middle ear cavities and might communicate effectively with airborne sounds throughout the *opercularis* system, which detects vibrations from the substrate. However, recently, two anuran species (*Brachycephalus ephippium* and *B. pitanga*) lacking tympanic membrane, extrastapes, stapes, and middle ear cavity – hence considered “earless” – are deaf to high-frequency signals, suggesting that these species are unable to perceive their own produced calls (Goutte et al. 2017).

## Morphological and Environmental Effects on Acoustic Signals

Noise is any unwanted sound that interferes with the detection of a signal and the information transmission, being a combination of non-biological or environmental noise (e.g., wind and turbulence) and biological noise (sounds from other animals) (Forrest 1994).

Many individuals of a different number of species using the same breeding sites could generate noise and become a potential problem (Stebbins and Cohen 1995). Heterospecific acoustic interference have diverged due to temporal characteristics of their calls (calling rate, call duration, call complexity, or the number of notes), spatial separation at breeding sites, and spawning and in other ways. Vocal divergence helps to ensure species recognition and reduces the chances of mismatings between closely related species and wasted reproductive effort serving as an efficient premating isolating mechanism (Forrest 1994; Ryan 2001; Gerhardt and Huber 2002).

Naturally, the sound’s pressure, intensity, and fidelity decrease the longer the distance it travels. The call can be attenuated and degraded, and the surrounding environment might impose a strong constraint on it by means of sound refraction, reflection, and absorption along the transmission path. Sound scattering and reflection also play a role in call degradation, defined as the decreasing of call integrity by losing definition in temporal traits and amplitude patterns. So, long-range communication must be efficient in order to overcome these issues. For effective mate attraction, the call should not only have sufficient intensity when it reaches the receiver to be detected, but it must also be discernible as a conspecific call (Ryan 1988; Forrest 1994; Wells 2007).

Habitat can differentially affect aspects of the calls. For instance, reverberations are almost completely absent in open habitats. On the other hand, signals in open habitats are prone to degeneration from different sorts of temporal interferences, like the wind (Ryan 1988).

The speed of a sound depends on air density and temperature. Sound travels faster in warmer air; thus temperature can influence spectral properties of calls. Temperature can be especially important when it affects properties of calls used by females to discriminate among sympatric species (Ryan 1988). Furthermore, anurans are ectotherms, and temperature influences those attributes of acoustic signals that are controlled by neuromuscular system (e.g., call, note, and pulse rates and durations) (Gerhardt and Huber 2002; Wells 2007; Köhler et al. 2017). Usually, researchers evaluate the strength of the association between environmental temperature at the time of recording and acoustic features by means of correlation tests or linear regression (Köhler et al. 2017).

The body size is usually strongly correlated with spectral traits, suggesting that fundamental and dominant frequencies are under morphological constraints. Since larger vocal cords are able to vibrate at lower frequencies and larger frogs usually produce calls at lower frequencies, vocal cord mass and length seems to be directly proportional to the frog's size. However, temporal traits have only rarely been suggested to be influenced by body size (see Bee and Gerhardt 2001). Besides the body size, call frequency can also be actively modified by changing the tension of the vocal cords associated with the contraction or relaxation of various muscles associated to the larynx (Gerhardt and Huber 2002).

## Social Interactions

Choruses are aggregations of acoustically signaling animals, formed by individuals of different species in areas where physical resources (within or along the margins of standing water in anurans) required by females to lay their eggs are present. Such behavior can reduce individual risks of predation making harder to find signaling individuals or by increasing the chances of predators being detected by some individual who then alerts the rest of the group. Chorusing increases the range of female's attraction since a group of signalers can be heard louder than single individuals at great distances. On the other hand, these aggregations intensify the competition among males to attract mates, to acquire and defend resources needed by female, or both (Gerhardt and Huber 2002).

Satellite behavior is a tactic in which males do not call while situated near a calling male, parasitizing the calling efforts of other males. This behavior usually depends on the individual's age, size, energy reserves, physical condition, signaling ability, and density of calling males. This tactic may be the only chance to mate for small, young, or weak individuals in species in which larger, established males hold territories and attack other males within or near their territories. Satellite males can intercept females that are attracted to the calling male, wait for the calling male to vacate its territory or calling site, or both (Gerhardt and Huber 2002; Wells 2007).

To avoid interference of overlapping conspecific calls, males commonly alternate their calls when close to one another, a behavior essential to preserve energy when high calling rates are emitted, particularly in those species that have prolonged breeding period and in which males are territorial.

## Honest and Dishonest Signals

Sexual selection encompasses the array of behavioral tactics used by individuals to acquire mates. Females select males as mates and represent a limiting resource and object of competition among males. Thus, males are subject to more intense sexual selection than females, and traits that enhance the ability of males to locate, attract, capture, or retain possession of females will be favored by sexual selection, as will traits that reduce the amount of time between successive matings (Wells 2007).

Honest signs transmit reliable information from sender to receiver. There is a general assumption of sexual selection that signals given by males to attract females tend to be energetically expensive to produce. Females often are attracted to males that emit long, loud, or high-rate signals, traits that are positively correlated with levels of energy expenditure (Ryan 2001). The energy cost usually keeps the signal traits honest and then reliable to receivers while assessing senders' information (Searcy and Nowicki 2005).

Besides the signal costs, constraints can influence in keeping signals honest. Given the physical body-size constraint of frequency in anuran calls, females and male competitors can interpret frequency traits as an honest signal portraying body size of the sender and, thus, its strength and quality. The fundamental frequency of calls is partially determined by the shape and size of laryngeal apparatus, which in turn is constrained by the body size (Bee et al. 2000; Wells 2007; Köhler et al. 2017). Thus, females and males rely on spectral properties of acoustic signals to assess male's quality and opponent's size during courtship and aggressive encounters, respectively (Bee et al. 2000; Köhler et al. 2017).

There are a few reported cases of dishonest signaling in anurans. In some species, males can alter call properties in order to emit a dishonest signal and be perceived as being bigger than they really are. For instance, in *Lithobates clamitans*, small male frogs can alter spectral properties during intraspecific interactions, emitting a dishonest low-frequency call when confronted by larger opponents (Bee et al. 2000).

## Visual Communication

Visual signaling is an alternative or complementary form of communication. This communication can be transmitted over relatively short distance and are often hindered by obstacles in the environment. This means distance (usually individuals need to be less than 50 cm apart) and light are restrictions for the communication process. This behavior may occur in both intra- and interspecific levels and is associated with reproduction (e.g., for female attraction), aggressive interactions related to territoriality, or predation and might be seen in males only or both males and females.

Species that breed at sites with high ambient noise levels, such as near waterfalls or torrential streams, might favor communication through visual display that either supplement or replace acoustic signals. Background noise might also be produced by other frogs and insects' vocalizations in species that breed in lentic water bodies (e.g., *Boana albomarginata*) and reduces the female's ability to discriminate among conspecific calls. The usual explanation is that the background noise makes vocal communication difficult; thereby close-range communication (visual and acoustical) is favored.

Foot-flagging or arm-waving displays might indicate agonistic contexts. Such displays are usually performed after conspecific males' approach or vocalize close a signaling individual. Once the first visual displays are performed, the outcome of interactions depends on the potential intruder. If the intruder calls, approaches further, or displays visually, the initial display is usually followed by further displays or physical combats. Initial displays or combats usually end when the intruder retreats. However, in some cases, the male starts to emit advertisement calls, and, when close to the female, he starts foot-flagging displays that presumably increase the female's excitation. The female may respond to the visual signal with the same display or with a different one (Ryan 2001).

Anuran vocal sacs are quite diverse in coloration and shape and have an important role in visual signaling. The change of vocal sac color during the courtship, known for some anuran species, suggests that it could play a role in visual communication. Gular inflation is synchronic with the call emission and may facilitate female localization of individual males in an aggregation. Even in species without distinctly colored vocal sacs, movements of the vocal sac may serve as a visual signal to other males or to females searching for mates (Rosenthal et al. 2004).

Visual communication can also be used in interspecific interactions. Aposematic signals as well as deimatic behavior are important and well-known anti-predator defenses. Deimatic behavior consists of intimidating postures or actions taken when caught by pursuing predators. It is usually associated with aposematic colors or a mimetic behavior. The *unken* reflex is a type of deimatic behavior in which the frog lifts all four legs and arches its back, drawing attention to the bright ventral surface. Such defensive behavior is effective in species with ventral warning coloration (e.g., *Bombina* and *Melanophryniscus*) (Ryan 2001). On the other hand, the eyespot display used by *Physalaemus nattereri* might be a tactic to mimic a bigger animal's body part such as a snake's head (Sazima and Caramaschi 1986).

## Chemical Communication

Chemical signal is the primary source of communication in salamanders (Caudata) and probably in caecilians (Gymnophiona). Historically, chemical communication has been presumed for many anuran species considering their skin permeability and the occurrence of physical contact during the amplexus (Rödel et al. 2003; Willaert et al. 2013). The first evidences suggesting the occurrence of this communication modality in anurans came from experimental studies on chemical perception (e.g., Rabb and Rabb 1963).

Tadpoles of many species are known to be able to detect chemical cues from predators (and injured conspecifics), conspecifics (to avoid intraspecific competition), heterospecifics, and relatives (kin recognition), which may active or passively release chemical compounds (reviewed in Belanger and Corkum 2009). In *Anaxyrus cognatus*, for example, posmetamorphic individuals aggregate possibly guiding each other by using chemosignals (Graves et al. 1993).

Part of the expectation for perception of chemosignals underwater is related to the known complex dual olfactory system of amphibians. Besides the main olfactory epithelium, which is more sensitive to airborne molecules, anurans have a vomeronasal organ (VNO; Belanger and Corkum 2009), which is more sensitive to waterborne molecules (Starnberger et al. 2014b). Apparently, the VNO develops and achieves early significant maturation in tadpoles in order to detect chemical cues in the water (Jungblut et al. 2012). For instance, tadpoles of *Kurixalus eiffingeri*, a Taiwanese rhacophorid tree frog, increase their activity in water conditioned by adult female or male, suggesting chemical perception of conspecifics (Kam and Yang 2002).

Chemical mate recognition and/or attraction based on waterborne substances has also been demonstrated for adults of some species. In the tailed frogs, *Ascaphus truei*, reproductive individuals show a preference for chemical cues from the opposite sex than those from the same sex (Asay et al. 2005). Females of *Ranoidea splendida* are attracted by "splendipherin," a waterborne pheromone produced in males' cephalic glands (parotid and rostral glands; Wabnitz et al. 1999).

Sexually dimorphic skin glands (SDSG; dermal macroglands often called "breeding glands"; e.g., Pearl et al. 2000; Willaert et al. 2013) have been reported for several anuran species (e.g., Brizzi et al. 2003) and recently their intra- and intersexual functions have been observed and/or tested (e.g., Pearl et al. 2000; Starnberger et al. 2013; Brunetti et al. 2014). Taxonomists have described and used presence and shape of conspicuous glands as a taxonomic feature for many anuran groups (e.g., Vences et al. 2007). Studies on reproductive biology of *Boana punctata* species group (i.e., *B. atlantica* and *B. punctata*), both in field and laboratory, described female contacting her snout to the flanks and gular regions of the male, where lateral and mental glands are located, respectively (Brunetti et al. 2014 and references within). Based on these observations and on the structure of the glands, it is suggested that the mental and lateral glands might produce substances used during courtship communication, as in many plethodontid salamanders (see Wells 2007).

In an experimental study, females of a dwarf African clawed frog, species of the genus *Hymenochirus*, show a positive chemotaxis to water with males or male's homogenized postaxillary breeding glands, whereas males of this species show no response to either water housing males or females, indicating a production of mate-attractant chemosignal (Pearl et al. 2000). On the other hand, the odorous mucus of both sexes functions as a sexual attractant in the terrestrial Australian toadlet *Pseudophryne bibronii* (Byrne and Keogh 2007).

In many anurans (e.g., *Leptodactylus* spp. and *Rana* spp.), males develop, as secondary sexual trait, keratinized spiny nuptial pads on the bases of the first fingers (i.e., thumbs) during the breeding season (reviewed in Brizzi et al. 2003). These nuptial pads usually have associated glands that would presumably produce glue-like substances to enhance the amplexus (Brizzi et al. 2003). Nonetheless, in *Rana temporaria*, these glands produce proteins structurally similar to those found in plethodontid salamanders, called “amplexins,” that might stimulate females to lay eggs. Apparently, these proteins could be delivered directly into female’s circulatory system through wounds on the female’s ventral surface, which result from abrasion between the male’s spiny pads and female’s skin during amplexus (Willaert et al. 2013).

Although rarer, some studies have reported male-male interactions stimulated by chemosignals (see Woodley 2015). For instance, males of *Leptodactylus fallax* produce a substance (*Leptodactylus* aggression-stimulating peptide; LASP) in their skin glands induced by intrasexual aggression (King et al. 2005). Males exposed to LASP become more aggressive, displaying behaviors such as jumping and rearing, whereas females had no response to LASP. Males of *Pseudophryne bibronii* avoid substrate marked by other males and react to this, switching from emitting advertisement calls to territorial calls after being exposed to other males’ chemosignals (Byrne and Keogh 2007).

Chemicals reported in aforementioned cases are peptides or proteins and then limited to be spread in water or through direct contact (Starnberger et al. 2013; Starnberger et al. 2014a; Willaert et al. 2013). Yet, a few studies also indicate communication via airborne chemical cues (see examples in Woodley 2015). Experiments with the American toad, *Anaxyrus americanus*, show male orientation toward volatile chemical cues obtained from females (Forester and Thompson 1998). Individuals of the poison frog, *Dendrobates auratus*, are attracted to the opposite sex based on olfactory communication (Korbeck and McRobert 2005). More recently, Brunetti et al. (2018) found that the sex-specific volatile components of the Neotropical tree frog, *Boana prasina*, are produced by bacteria of the genus *Pseudomonas* present in the frog’s skin. Biochemical and histological analyses of the gular glands of 11 species of 4 hyperoliid genera demonstrated males as capable to produce volatile compounds (Starnberger et al. 2013; reviewed in Starnberger et al. 2014a, b). These glands are located at the gular region of the tree frog males, forming a distinct patch on the inflated vocal sac during calling activity. Moreover, there is a huge compound diversity (65 different types) in species-specific chemical combinations (Starnberger et al. 2013). It has been suggested that these compounds might be actively fanned out and spread into the air by vocal sac pulsations, while males are calling, functioning as a chemosignal in a multimodal communication to species recognition and mate choice (Starnberger et al. 2013, 2014a, b). Species-specific communication via volatile chemosignals is also likely in mantellid frogs from Madagascar (Poth et al. 2013). Males of many mantellid species have distinct femoral glands (Vences et al. 2007), which produce airborne chemicals capable of increasing individual activity in both sexes (Poth et al. 2013).

## Tactile Communication

Pre-mating touching between male and female has been reported for some species, such as *Aplastodiscus* spp., *Hylodes* spp., *Bokermannohyla ibitiguara*, *Boana atlantica*, *B. punctata*, *B. faber*, and *B. rosenbergi* (Brunetti et al. 2014, de Sá et al. 2016; and references within). For many of these taxa, the amplexus only occurs after female physically contacts the male (see Brunetti et al. 2014; de Sá et al. 2016). Females of *Hylodes japi* can repeatedly touch the posterior part of male’s body out of his sight during the courtship behavior, inducing him to emit courtship calls, which suggests the tactile signal as the single stimulus in this case (de Sá et al. 2016). However, for most cases, occurrence of chemical or visual communication during the physical contacts cannot be excluded, making the presence and extension of mechanical stimulus not clear (Brunetti et al. 2014). Moreover, tactile communication studies have failed to fully explain how information can be coded into and assessed from the signals. For instance, in *Boana rosenbergi*, female choice seems to be likely based on differences of male's physical contact. However, how exactly females assess a male's quality through physical contact and what are the preferable signal traits are not known (Kluge 1981).

Tactile stimuli are also frequently observed when tadpoles beg for unfertilized eggs in species with maternal egg provisioning (e.g., Kam and Yang 2002; and references within). Tadpoles of dendrobatid strawberry poison frog, *Oophaga pumilio*, stop swimming and start vibrating their bodies when close to the parents (reviewed in Dugas 2018), while tadpoles of the rhacophorid tree frog *Kurixalus eiffingeri* also nip the skin of mother's cloaca and thighs (Kam and Yang 2002).

## Multimodal Communication

Multimodal communication refers to the cases where the signals are produced and received using two or more sensory modalities. Although anurans have, as well as for most animal taxa, their predominant modality (i.e., acoustic communication), a growing amount of evidences has demonstrated the occurrence of multimodal signals (usually composed of an acoustic signal plus a visual or chemical one; see above). Four information content hypotheses have been proposed for additional components in anuran communication. They may be (1) useless such as in signals produced by-product (epiphenomenon), (2) redundant in relation to that present in the primary modality (i.e., components possess similar information but only one is necessary), (3) complementary as a reinforcement for signal perception by receivers (they make the whole signal more conspicuous to receivers but are still not necessary), or (4) essential as subcomponents of a complex signal, which, if decomposed, would not be perceived by receivers during communication (de Luna et al. 2010).

The different components of the apparent trimodal communication (chemical, visual, and acoustic) of the hyperoliid species might function as redundant stimuli for females (Starnberger et al. 2013). Since these tree frogs usually breed in a multi-species context (i.e., several species communicating and breeding at the same time and space), redundant signals emitted through different channels and sensory systems might facilitate recognition and locating of conspecific males (Starnberger et al. 2014b). In *Engystomops pustulosus*, extra sensory modalities are not necessary for female attraction but may be beneficial for sender while increasing efficacy and conspicuousness of the signal and for the receiver as acting as additional cues to assess male's quality during mate choice (Taylor et al. 2011). Although female tactile stimuli only stimulate males during courtship interactions, a combined bimodal (visual + tactile) signal can be threefold more stimulating than separated ones (de Sá et al. 2016).

Evidences of whether each signal component is important as stimulus come from experimental studies. For example, territorial and aggressive *Allobates femoralis* males only attack other males if a bimodal signal (acoustic + visual) is produced, i.e., there is no reaction in cases with a single modality only (either visual or acoustic; Narins et al. 2003; de Luna et al. 2010). In this species, both sensory modalities seem to act as nonredundant components (de Luna et al. 2010). Initially, the required visual component was attributed to the pulsation of the vocal sac during calling (Narins et al. 2003). However, de Luna et al. (2010) found that body movement can instigate the same aggressive behavior, suggesting that any individual movement can function as an additional component to the acoustic one.

## Conclusion

Anurans primarily communicate intra- and interspecifically through acoustic signals. Males inform their position, readiness, and status to rival males and females. The assessment of male's quality by female is particularly important to species-specific recognition and sexual selection, since females of many species choose mate mainly based on acoustic signals (Gerhardt and Huber 2002; Köhler et al. 2017). Although these signals are the most conspicuous, other communication modalities have received more attention from researchers who have demonstrated them as being more widespread and important within the order than originally thought (Starnberger et al. 2014a, b).

As well as in the acoustic modality, visual and chemical communications occur in both male-male agonistic interaction and male-female mate choice (review in Ryan 2001; Woodley 2015). However, in species with repertoires composed of different signal modalities, regardless of whether the signals are obligatorily synchronized or not, each sensory channel seems to be used in a different phase of the behavioral event. According to field observations, initial phases of the courtship and aggressive interactions usually occur at significantly long inter-individual distances and, therefore, are similarly dependent on long-range signals such as sounds, whereas final phases of these interactions tend to occur at closer distances, allowing the use of typical close-range signals such as in chemical, visual, and tactile communication (see Pearl et al. 2000; e.g., Starnberger et al. 2013; Brunetti et al. 2014; de Sá et al. 2016).

Even in synchronous multimodal signals, each of them may play a different role and be used for a slightly different purpose in intraspecific communication. In most species with acoustic, visual, chemical, and tactile signals, the former and the latter occur in a long- and close-range communication, while the rest tend to occur at intermediate distances, in short-range interactions (Starnberger et al. 2014a).

Although non-acoustic communications have been historically neglected in the order, the number of reports of chemical, seismic, visual, and tactile signal, during intra- and interspecific interactions, has been growing in the past three decades (Ryan 2001; Starnberger et al. 2014b; Woodley 2015; Köhler et al. 2017). Therefore, we expect to see a significant number of new cases related to all these modalities in the anuran communication literature in the next decades.

## Cross-References

- ▶ Auditory Signals
- ▶ Behavior Systems
- ▶ Call
- ▶ Chemical Signals
- ▶ Communication
- ▶ Displacement Behavior
- ▶ Honest Signalling
- ▶ Reproduction
- ▶ Reproductive Strategy
- ▶ Reproductive System
- ▶ Salientia Cognition
- ▶ Salientia Communication
- ▶ Salientia Diet
- ▶ Salientia Life History
- ▶ Salientia Locomotion
- ▶ Salientia Navigation
- ▶ Salientia Sensory Systems
- ▶ Secondary Sex Characteristics
- ▶ Sex Differences
- ▶ Sexual Attraction
- ▶ Sexual Dimorphism
- ▶ Sexual Identification
- ▶ Sexual Selection
- ▶ Social Behavior
- ▶ Sociobiology
- ▶ Sociosexual Behavior
- ▶ Species-specific Behavior
- ▶ Symbolic Communication
- ▶ Visual Recognition
- ▶ Visual Recognition of Prey and Predators

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