COMMUNICATION SYSTEMS IN TROPICAL TERRESTRIAL VERTEBRATES: AN OVERVIEW

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Summary

The functionality of communication systems depends upon a set of minimal elements: a sender, a receiver, a channel, and a signal repertoire common to both sender and receiver. In many cases this basic system does not reflect reality because usually there are multiple receivers and senders acting simultaneously. These complex communication systems are addressed by the communication networks theory, which predicts many behavioral consequences resulting from the interactions of multiple senders and receivers. There are at least five different communication channels that could be used by terrestrial animals to send information to other individuals: chemical, visual, acoustical, tactile and seismic. Each one of the channels has some idiosyncratic characteristics. Nevertheless, it is important to stress that animals usually express

signals in more than one channel at a time, a phenomenon known as multimodal communication, and the effects of these signals can be different in many ways. Animal signals are used in different habitats, and exposed to the action of different kinds of degrading agents. These factors are generally known as "noise", and this noise could constrain the characteristics of the signals being propagated in different habitats and through different channels in many ways. Signals are, then, constrained by this influence and suffer evolutionary changes in design to adapt and cope with these interferences. Constraints could be mainly of two types: environmental (including vegetation, soil, rocks, temperature, wind, humidity, etc. or biological. The latter includes all animals signaling in the same channel as a given sender, from the same or other species, from which interfering emissions could occur. These sources of constraints acting in tropical environments will be discussed here. Finally, some examples of communication systems from the tropics will be presented and discussed.

1. General Features about Communication Systems

Communication systems have, for a long time, attracted the attention of both naturalists/scientists and curious people. This interest is based not only on the particularities that animal communication systems exhibit but also in the differences and common traits we find when comparing them to our own means of communication. From Aristotle's interest in the sounds produced by fish and dolphins, to the curiosity expressed by musicians and naturalists about bird song (leading to attempts using musical notation to characterize bird song) to the present interest in how animals communicate, the understanding of animal communication systems has taken a long time to reach the "state-of-the-art" knowledge of today. This interest has come mainly from scientists but also has reached the general public through documentaries and books. Even if we know now more than we knew some years ago, we are still far from a full understanding of all the modalities and nuances implied in communication, both in humans and in other animals. Many of the expectations relative to understanding animal communication systems reflect our desire of grasping the evolutionary history and full comprehension of our own communication system that is not reduced to verbal communication.

Nevertheless, understanding communication systems is not only important as a way to understand ourselves, but also is important in itself because any kind of cooperative activity –and even many non-cooperative ones- depend on the existence of a basic and reliable communication system. Even those animal species that live solitary existences have to deal with inter-individual activities like reproduction and offspring care that demand some intra-specific contact and coordination, which can only be achieved through the use of a communication system. This characteristic of communication systems makes them very valuable as a tool to understand other areas of animal biology and behavior associated with social structure and cognitive abilities. Social structure relies upon established communication systems, and if we can understand the communication signals and exchanges that animals of a species use to establish their "social network", we will be able to understand the social network itself. On the other hand, complex communicative tasks are usually demanded by complex social organizations, which usually demand complex cognitive abilities for participating in a social network. Thus, scientists can use communication systems as a window through which they can take an "inside look" into other areas of animal behavior.

Many fields of learning partake in studies of communication, including ethology, physiology, neurobiology, ecology, taxonomy, paleontology, semiotics, physics, and chemistry, among others. These fields and others are needed to gain a full understanding of the structure, function, ontogeny and phylogeny of communication systems. Indeed, ethology (or behavioral ecology) is the chief domain for this task because it is the one that tries to draw the most comprehensive picture of communication systems and their functioning in the "real world", subject to the constraints imposed upon animals when they transmit (or share) information in "real world" animal populations.

1.1. Communication Systems Basic Features

There is a minimal set of elements that should always occur in any functional communication system: a Sender, a Receiver, a physical way of transmission for the signals, usually known as a Channel, and a signal Repertoire or Code (Figure 1). Sender and Receiver are usually animals of the same species, but interspecific communication has been documented in many opportunities and could potentially appear also in a simple system like the one we are describing now. The Sender is the individual that emits the information and the Receiver is the individual intended by the Sender to gather that information and, eventually, use it.

Figure 1. Schematic representation of the basic components of the simplest communication system.

The Channel is the physical way used by the Sender to encode information for transmission to the Receiver. Animals use different channels depending on their sensory arrays. The use of their senses in a task that implies gathering external information is not surprising because it is the sensory organs' main function. Additionally, different parts of the nervous system are used in the related information processing systems, which is used to collect and analyze external information for the subject to use.

Obviously, the use of certain sensory capacities for communicating assumes that the species in question have both emitting and receiving organs able to cope with the communication task when using a particular channel of communication. In essence, the sensory abilities needed by the animals to communicate in a given channel do not exceed the capacities of their own sensory systems, because animals use only a part of the possibilities of their senses to communicate while the rest of their sensory abilities are used in other information gathering tasks like finding food, detecting predators or shelters, etc.

The Repertoire is a group of signals that is considered to have evolved with the function of transmitting or exchanging information between Sender and Receiver. These signals have encoded information and both Sender and Receiver have to share that repertoire and coding/decoding rules to allow mutual understanding. An immediate example of a repertoire is human spoken languages. Each language or variant has a system of signals that encodes information (words) even when using the same system of symbols from which to elaborate an alphabet. If the Sender and the Receiver share the same code (language rules and/or set of meanings) they can understand each other, but if they do not share the same code they will not be able to talk. Even a partial knowledge of the code (repertoires shared in part) will allow some kind of communication, but if the repertoires are not shared (as in the case of people speaking in different languages) communication is almost impossible, except by way of other shared repertoires (gestures or non-verbal communication). The use of multimodal signals will be addressed later in the text.

This simple system is activated when an animal (Sender) emits a signal to the external medium, intended to be gathered by a designated Receiver, usually of the same species. The signal used should be part of the Repertoire and is encoded with certain kind of information. That information will travel through the external medium and (probably) be gathered by the intended Receiver. The Receiver should detect the signal, “assimilate” it and decode it through the use of its sensory receivers and processing parts of the nervous system. Subsequently, the Receiver usually considers the information received and carries out some activity, completing then the functioning of the system.

It is important to stress at this point that the actions performed by the Receiver are the usual, and sometimes the only, way for an external observer to detect that a communication has occurred, and also represents the key opportunity to interpret the meaning of the emitted signal. Nevertheless, receivers do not always react immediately to the reception of a signal, nor in a way we can readily understand or sample. Indeed, sometimes they do not react at all because that was the intended meaning of the signal, or because their reaction is purely internal (physiological or “mental”, e.g., a change of sexual hormonal levels or a change in the awareness level of the subject), or even because they did not detect the signal at all.

In any natural communication system there is always another element, purposefully neglected until now, but which is very important given their consequences upon the functioning of the systems. This element is called Noise, and is present in almost all biological communication systems. Noise is not only a sound matter, but could be defined as any interference that tends to impair or destroy the signal when it is traveling between Sender and Receiver, i.e., the leaves in trees that interfere with the reception of a signal emitted through movements, or a strong wind that overdisperses an animal’s scent. Many of the characteristics exhibited by communication systems and many of the constraints they should overcome are determined by the existence and nature of Noise. Thus, during the evolution of most biological communication systems different strategies have evolved to eliminate or at least diminish the destructive action of noise. These kinds of strategies are studied today and identified in some of the characteristics of the signals themselves or in the way they are emitted. These characteristics are part of the set of rules for signal construction known as Signal Design. Each kind of signal has different design characteristics depending on the type of meaning or information it conveys, the kind of noise and /or external or internal constraints to which it is subjected, and also depends upon the repertoire of a given species.

Why animals refine their signaling systems during evolution to cope with noise? There are many reasons for this process, but two reasons stand out:

- Using a signal or succession of signals that can overcome the action of noise to deliver the most complete version of the information emitted to the Receiver;
- Reducing the costs of communication to a minimum.

Communication is costly and information sharing or exchange has costs both for senders and receivers. Some of these energetic costs are associated with the following:

- direct production and coding of the signal by the Sender;
- structures needed to produce the signals by the Sender;
- need to overcome noise by the Sender;
- signal detection by the Receiver;
- decoding and analysis by the Receiver;
- production and maintenance of the structures and systems needed for reception and analysis by the Receiver;
- engaging in communication and decreasing the time dedicated to other important behaviors (e.g., feeding, mating, antipredator vigilance) for both Senders and Receivers.

Based upon the above, we can understand why animals try to optimize their signals and communicative exchanges in ways that allow them to obtain the highest benefits while investing the lowest effort.

1.1.1. Communication Networks

The system described before could be considered complete, but in the majority of cases this basic system is much too simplified to reflect reality. Usually there are multiple receivers, and probably also multiple senders acting at the same time and location, and these complex communication systems are addressed by the Communication Networks theory. This body of theory assumes that when animals use channels that provide long-range signals, there is always more than one Receiver, and probably more than one Sender acting simultaneously (Figure 2). Theory thus allows us to predict many behavioral consequences of the intervention of multiple senders and receivers on the signals and repertoires used.

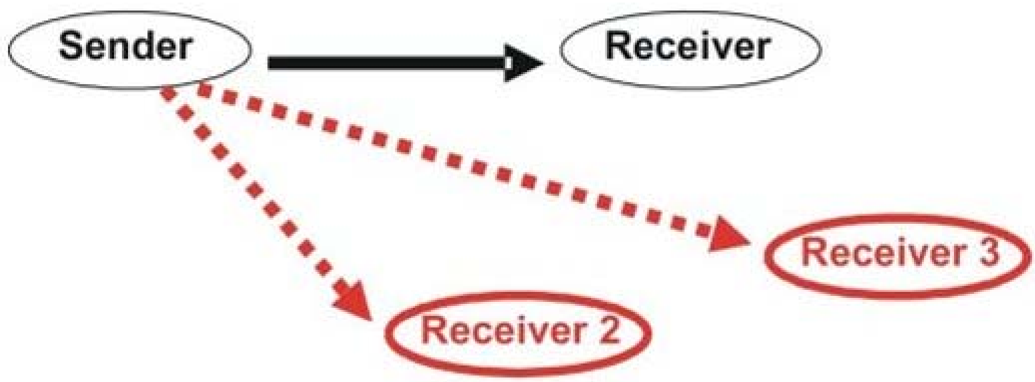

Figure 2. Schematic representation of a simple communication network. Receivers in red are unintended (possible eavesdroppers).

We can define long-range signals as those that can travel farther than the mean distance usually separating two individuals in a population of a species in question. If we use the Communication Network Theory as the better representation of the real communicative interactions when animals use such long-range signals we have to take into account the highly probable situation of many "unintended" receivers gathering information from a signal delivered by a Sender with the possible destination of only one conspecific.

Assuming that this is true, some immediate consequences arise:

- Some unintended receivers (eavesdroppers) will gain information not intended to them;
- Senders could try to avoid this effect by "privatizing" their signals. This means, formatting the signals to avoid the possible eavesdroppers (e.g., a bird decreasing the loudness of its song so that the song will only be "available" to a restricted group of receivers in the vicinity of the sender);
- Other Senders will "put the system to work for them" by increasing the power or detectability of their signals ("publicizing") to attain more receivers than those supposedly intended by the signal;
- The decision to privatize or publicize signals depends on whether the Sender knows which receivers it may reach; this is known as the "Audience Effect". If the Sender knows some characteristics of its audience, it could better modulate (regulate) the signal output and avoid eavesdroppers or manipulate receivers;
- Some receivers, both intended and unintended, could use their own signals to stimulate a Sender to continue emitting and even to increase the amount of information encoded in their signals. When these receivers are emitting in that context we say they are "announcing" themselves.

It is evident that when interpreting the meaning of animal signals or when trying to understand how communication systems work, we have to take into account all the factors mentioned above. These will determine in many cases the signal design and the use of one particular communication channel over others Thus, the nature of a communication system influences or constrains how we study these systems. When we examine some real communication systems in nature, we will emphasize these kinds of influences and develop these concepts by analyzing some examples in depth.

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Biographical Sketch

Gabriel Francescoli is Adjunct Professor of Ethology at the Ethology Section of the Animal Biology Department, Facultad de Ciencias (Universidad de la República, Montevideo, Uruguay). After his degree in Uruguay he has done his D.E.A. at the University of Paris V (1984), and then completed his doctoral studies in the PEDECIBA Program in Uruguay (1998). His main research interests are animal communication systems, especially acoustic and vibrational communication, and subterranean rodent communicative and behavioral evolution.