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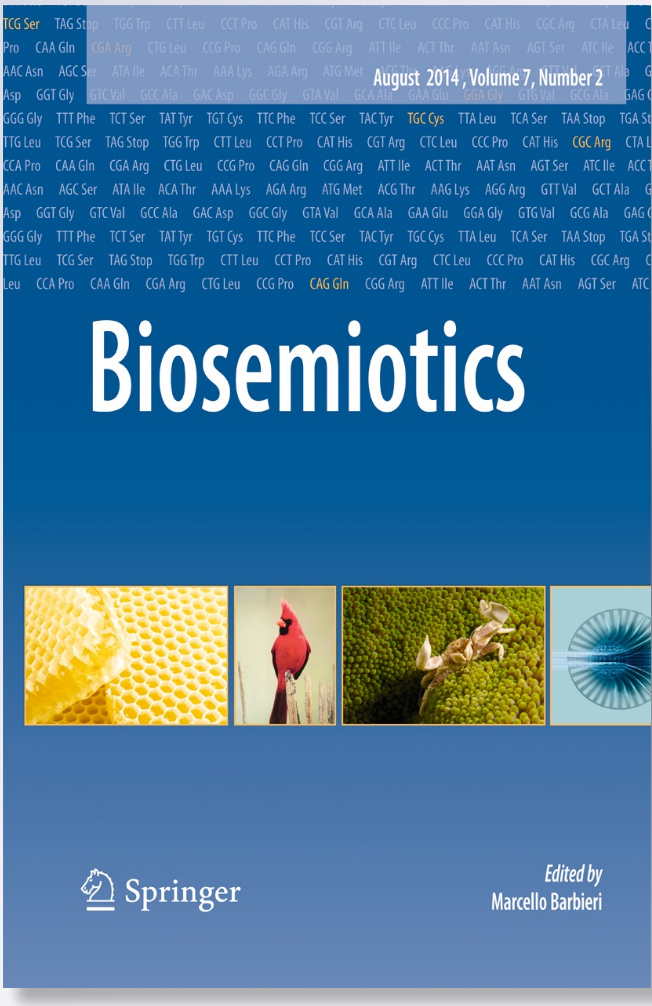



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ORIGINAL PAPER

# Acoustic Codes in Action in a Soundscape Context

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**Abstract** Acoustic codes assure the intra and interspecific communication of vocal animals. They are composed by a sequence of nominal entities (syllables, words and sentences) and by magnitude modulation confirming in such a way contemporarily a behavioural and ecological nature. The acoustic codes find evidence in the acoustic niche hypothesis by which species in order to reduce interspecific competition (acoustic overlap) occupy a restricted portion of the available frequencies modulating very precise acoustic cues (codes). Their evolution, like other aspect of biology, is under control of the environmental conditions assuming the more favourable configurations. These nominal entities respond also to the amount of energy by which are emitted allowing to the eavesdropping individuals to range the distance at which a potential competitor is broadcasting a signal. Environmental alterations, especially if of anthropogenic origin, can produce severe consequence of the acoustic codes that in turn may affect the prey–predator balance and the complexity of communities. In fact acoustic codes under an environmental constraint like human noise intrusion can be modified in order to reduce a masking effect, demonstrating their phenological plasticity. The new ecological discipline of soundscape ecology offers the possibility to investigate the nature and the evolution of the acoustic codes in different environmental conditions.

**Keywords** Acoustic codes · Birds · Soundscape · Acoustic niche · Ranging · Masking

## Introduction

The ecological complexity of natural systems is the result of the interactions between landscapes, ecosystems, animal communities, populations and individuals. Most of these interactions operate according to a thermodynamic gradient (Odum 1983), whereas others are characterized by a neg-entropic regime (Schrödinger 1944), by a dramatic increase of the flux of information (Reza 1961) or by distance from a high-probability state of entropic configurations (Ulanowicz 1997).

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At first sight, a complex system is perceived as a complicate one, but this is a misleading effect largely due to a lack of understanding of the rules that govern the relationships between its component parts. Such rules are driven by sequences of 'ecological' codes that are used to connect at least two subjects allowing specific information to transit.

Like all organic codes (Barbieri 2003, 2013) the ecological codes can be defined as mechanisms that establish an arbitrary set of connections between two or more components (organisms and/or their aggregations) of a complex system. They represent the tools that organisms use in everyday life to relate themselves with the external world realizing a two-way path, and emitting and absorbing some parts of the information that is present in the surroundings. Ecological codes consist in visual, acoustic, tactile, chemical and cultural cues that exist at every scale of the living organization from individuals to meta-communities and over.

More functions require more ecological codes, which results in further possibilities for the organisms to interact with the external environment or Umwelt, sensu von Uexküll (von Uexküll 1982; 1992), and to finally benefit for resources (Farina 2012).

The ecological codes transform external objects and process analog gradients into discrete meaningful digital units. In birds, for example, the distance from a safe place is transformed into discrete-distance-units, each associated to a specific habit (e.g. stay confident, quickly escape, alerting, etc.). Such transformations are performed by cognitive code-makers and produce codes that are incorporated into the genetic or the cultural reservoir of every organism along an evolutionary process.

The ecological codes are associated to distinct functions that in turn are activated by a specific physiological need. A physiological need is a signal regarding the lack or deficit of a specific substance or of a behavioural trait. For every function there is a dedicated code sequence that guides to tracking the resource requested to satisfy a specific need. The dance of honeybees is an example of a very detailed and specific codification about food source and abundance. The need to assume food is performed by a predator by using a search image of the prey as a result of which the right prey is selected and every other organism excluded. For example, an insectivore bird has a codified (cognitive) image of the prey that suits it.

A food specialist has a restricted repertoire of 'cognitive templates', which allows it to save energy, whereas a generalist has a broader collection of templates that leads it to waste more energy in random attempts to gain food. More complex codes are required to optimize the search for resources. In addition to the codes for recognizing a prey, for example, there are codes for identifying the suitable environment in which to search for a prey. To every resource it is associated a spatial configuration that is a carrier of meaning—see the theory of the eco-field (Farina and Belgrano 2006)—that must be recognized.

Today, land degradation, overexploitation or climatic alterations have changed the environmental conditions in which ecological codes have gradually evolved together and have become crucial issues in the challenge to preserve biodiversity and the associated ecological processes.

In the present paper, our interest is focused on the domain of the acoustic codes and more in general on the ecological codes used in a soundscape context. In particular, our aim is to illustrate how in animal communication, and in particular in birds, the behavioural and ecological codes are essentials.

## Behavioural Versus Ecological Codes

Codes are fixed in the genetic heritage of every species but it is possible to distinguish sub-categories of codes according to the context in which they are working. For instance behavioural codes act inside the change of body posture, acoustic modulation and finally in movements of individuals in a physical context (see f.i. Byers 1996). Behavioural codes regulate the relationship between individuals in a species but can be extended also to interspecific relationships.

Ecological codes are based on a reactive system modulated by thresholds in energy or matter. For instance, an organism is recognized by a predator as a prey only if its size belongs to a specific range of body size. Similarly, the distance from a refuge is dynamically coded by a threshold of risk.

The ecological codes are comprised in the epistemology of the ecological niche (Hutchinson 1959). In fact the ecological niche describes the threshold at which an organism recognize a 'favourable' context in which operates for every function it uses, because for every vital function there is an optimum condition in which this function operates, below and above this interval such function cannot operate and the context becomes hostile or incompatible.

## The Acoustic Codes

The acoustic codes have been recently defined (Farina 2014) as units of informational acoustics carried out by special organs (e.g. syrinx in birds, vocal cords in humans, tymbals in some insects) with specific sequences (song, contact calls, alarm calls, etc.) to produce meaning and have a bivalent nature (behavioural and ecological). Acoustic codes are the result of indivisible units that compose the alphabet in the sonic language. The acoustic codes exist not only at intra-specific level but also (although partially) at interspecific level. The presence of interspecific codes has been demonstrated in several cases in which the acoustic performance of one species is used for some purpose by other species. This last fact creates the condition for an interspecific coordinated aggregation of acoustic cues that recently Farina and Pieretti (2013) have called *soundtope*. This creates favorable conditions for the organization of interspecific exchange of information often invoked as proof of the existence over the population level of a community level. Monkkonen et al. (1990) coined the term 'heterospecific attraction' to describe the phenomenon by which a species prefers to settle near other species with similar ecological niches. The acoustic codes are structurally complex in songbirds and in some terrestrial and marine mammals, and relatively simple in frogs and fishes.

## The Nature and the Mechanisms of the Acoustic Codes

The acoustic codes are distinguished sequences of syllables like in the alphabetic vocabulary. Every sequence is a letter and the combination of different letters create a phrase and a meaning. This happens in animal communication as well as in human language, but with the differences that in non-human animals the complexity of the acoustic signals is produced by the frequency modulation that act in a fixed way. In other words, the acoustic codes of the majority of animals are restricted to fixed sequences that cannot be either modulated neither combined to create a true language. For instance, call and song are the two typologies of acoustic codes in the majority of singing birds: calls are simple sequences in a narrow frequency band, song is the result of modulation in frequency and intensity and usually has a species-specific complex structure (Marler and Slabbekoorn 2004).

As illustrated in Fig. 1, a code is created either by a specific string (A, B, C) either by the repetition of the sequence (AAAA, BBBB, CCCC) in which the number of iterated calls represents a signal per se. Long iterated calls mean a condition of alarm or difficulty of the broadcaster. In birds, alarm calls are frequently uttered by adults that have young fledging to take care of.

Another additional coding possibility is represented by the magnitude of the acoustic cues (like AAAAA, Fig. 1). The amount of energy that the organism uses to produce a vocalization depends upon its internal physical condition (the theory of the honest signal, see a review by Andersson 1994, and Gil and Gahr 2002) or by behavioural motivations and levels of stress. This has been demonstrated in frogs where the loudest males are the ones preferred by females (Márquez et al. 2010).

## The Acoustic Niche Hypothesis

The acoustic niche hypothesis states that, in order to reduce interspecific competition and loss of energy, because vocalization is a costly exercise (Zollinger et al. 2011), every species produces vocalizations (alarm and contact call, song) inside a precise frequency range. This allows to distinguish a species from another also when they vocalize contemporarily (Krause 1993). The acoustic niche hypothesis has been considered as an adaptive mechanism of species within the evolution of the habitats


**Fig. 1** A code can be expressed simply as a distinct signal (**A**, **B**, **C**) or as a repetitive signal (f.i. AAAAA) or as magnitude modulation of a signal (f.i. A to A) or by a sequences (**A B C**)

(ecological succession, disturbance) and the interval of time during which species have coexisted, as recently pointed out by Malavasi and Farina (2013). The acoustic niche hypothesis is definitively based on the presence of specific acoustic codes that reduce uncertainty in the messages that every species utters. For instance, when the environmental conditions change, for a climatic shift or for an invasive processes, some problems of communication can be created in the communities.

We report as example the recent invasion of the Red-billed Leiothrix (*Leiothrix lutea*) along the Thyrrhenian coast of Northern Italy (Farina et al. 2012). This species has a strong acoustic overlap with Blackcap (*Sylvia atricapilla*) and it seems that the latter avoids acoustic competition by moving far away from the Red-billed Leiothrix's new established areas. In playback experiments in areas recently colonized by Red-billed Leiothrix, Farina (*personal communication*) has observed how the Blackcap sings only in the interval between two song sequences of Red-billed Leiothrix (Fig. 2). This acoustic subordination of the Blackcap can be interpreted as an attempt to reduce interspecific competition and to maintain a conspecific acoustic contact. But, according to an evolutionary perspective, the Blackcap should have two chances: either overlap its song with that of Red-Billed Leiothrix and try to discourage the intruder with an aggressive behaviour or, as it seems the case, sing in the acoustic space left free by the Red-Billed Leiothrix.

## Acoustic Code and Environmental Adaptation

Acoustic codes are used by numerous species to communicate. Their complexity depends on the adaptation of the species to the environment. In environments where the biodiversity is very high, such as the tropics, acoustic codes are highly differentiated and occupy a narrow space in the spectral window. The compression of these codes demonstrates the plasticity of the species to coevolve in a complex system where intra and interspecific competition are strong. Code ontogenesis is strictly correlated with habitat conditions. According to the Acoustic Adaptation Hypothesis (Morton 1975) species modified their acoustic repertoire in order to minimize the masking effect of vegetation. In this way, high frequencies are used by species living in open habitats, and low frequencies are very common in animals living in densely vegetated habitats as experimentally proved by Brown and Handford (2000) and Naguib (2003).

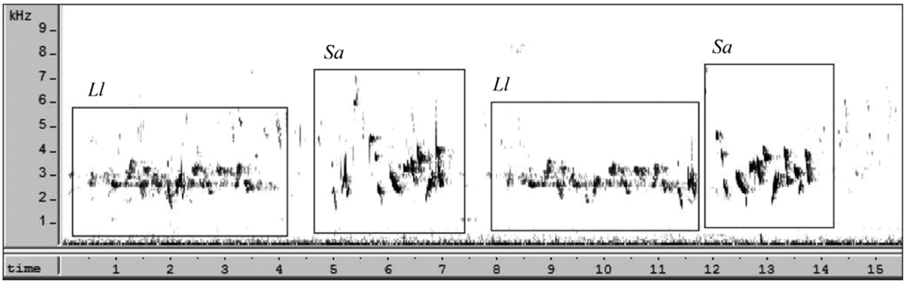


**Fig. 2** Acoustic interaction between Blackcap *Sylvia atricapilla* (*Sa*) and Red-billed Leiothrix *Leiothrix lutea* (*Ll*). Playback experiments have demonstrated the capacity of *Sa* to "fit in" where the *Ll* is not singing

## Ranging When Code is Based on Distance from the Acoustic Sources

Ranging is a process of evaluation of the distance from which a signal is broadcasted. This process requires a specific codification of the signal in order to produce a correct interpretation by a receiver. In general, ranging is particular useful in forest habitats where the visual cues cannot be utilized and the acoustic signals remain the most important way to communicate. Ranging process is utilized to estimate the degradation of the acoustic signal produced by soil morphology and vegetation cover that severely affect the quality and consistency of acoustic communication. Ranging is common in territorial birds and vocal mammals and is a strategy to save energy while defending a territory.

The ranging hypothesis has a more complex patterns than expected: for instance familiar signals are more detected than unfamiliar ones. This has as consequence that a degraded and unfamiliar signal could be less detected, thus escaping the direct ranging. Ranging process is based on the distinction between far signals (background) and close signals (foreground) by an eavesdropping subject. The individual reaction and its spatial displacement in a patrolled area largely depend by the capacity to distinguish an intruder, and this fact requires a prompt reaction, while from a transient or distant competitor this condition does not elicit a direct action. For instance, the ranging behaviour of Chaffinch (*Fringilla coelebs*) has been studied by Naguib et al. (2000). This author has exposed wild individuals to song playback broadcasted at distance of 0, 20, 40, 80 and 120 m demonstrating the capacity of the Chaffinch to react according to the distance of the potential competitor. In ranging behaviour the coding process is based either on specific song or on the level of loudness at which the first is perceived. The duality of the coding process seems confirmed.

## Masking Effect and Acoustic Codes

The acoustic communication can be at risk when an unwanted sound (noise) masks a signal reducing its role and effects. It is well know the effect of noise on human voice, known as the Lombard effect, from the French ear specialist Etienne Lombard that discovered this phenomenon (Lombard 1911). This effect consists in a shift of magnitude of the signal under a noisy context in order to be better heard. In nature there are several examples of reaction to the masking effects along an adaptive process, observed, for instance, in the Concave-eared Torrent Frog (*Amolops tormotus*) a species of arboreal frog of Central China that has ultrasonic harmonics used to communicate in a noisy environment (Narins et al. 2004).

The masking effect has long term evolutionary effects but also short term adaptation demonstrating the capacity of many species to have plastic attitudes. Slabekoorn and Peet (2003) have observed in Great tit (*Parus major*) populations a shift toward higher frequency bins in urban populations living in noisy conditions. This effect has been also observed on Zebra finch (*Taeniopygia guttata*) by Cynx et al. (1998).

When birds were subjected to various levels of white noise, it was observed a significant increase of the amplitude level of their vocalizations. The increase of sonic human intrusion into natural environment and especially in urban areas has forced many animals to change habits and to modify their communication patterns, demonstrating that acoustic codes have a strong component of phenological plasticity and definitively, although fixed in the genetic bank, have a significant margin of variability.

## Conclusions

Acoustic codes are the basis of communication in the majority of vocal animals especially during the delicate and strategic period of reproduction. They are fundamental to guarantee intra and interspecific relationship between species, concurring to the survival of populations and to the organization of communities. Like all other biological codes, they are the result of a process of adaptation to the local context where habitat conditions and interspecific relationships are the major proxies. The acoustic codes demonstrate that vocal animals apply a common strategy to save energy during the access to material or immaterial resources (sensu Farina 2012) adopting biosemiotic mechanisms.

Acoustic codes are the basis of animal communication processes and their manipulation by direct (noise interference) or indirect (climatic changes, habitat fragmentation) human intrusion can produce dramatic changes in the semethic relationship (*sensu* Hoffmeyer 2008) between species altering prey–predator equilibrium and/or key-stone species roles.

The investigations of the acoustic codes as part of code biology (*sensu* Barbieri 2013) have great possibilities to be developed and tested with a rigorous procedures based either on the analysis of observed patterns and on the experimental simulation and manipulation, via playback, of natural conditions. This investigation has been recently powered by the soundscape ecology, a new ecological discipline (Pijanowski et al. 2011a, b; Farina et al. 2011a, b; Farina 2014) that offers the possibility to investigate the evolution of the acoustic codes in different environmental conditions and their 'phenological' plasticity in an environmental context in which variability and unpredictability are recently dramatically raised.

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