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Are communication activities shaped by environmental constraints in reverberating and absorbing forest habitats?

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ABSTRACT

In the dense vegetation of temperate or tropical forests, communication processes are constrained by propagation-induced modifications of the transmitted sounds. The presence of leaves, trunks and branches induces important sound reverberation and absorption leading to diminution of the signal energy as well as qualitative modifications. The aim of this paper is to briefly review the different strategies used by birds to manage with these constraints. At the emitter's level, an adapted emission behavior which takes into account both the physical heterogeneities of the forest environment and the temporal variations of the acoustic constraints, is especially useful to control the active space of signaling. The coding of information into acoustic parameters that have different susceptibility to propagation constraints is also of great interest. At the receiver's level, an adaptive reception behavior (listening post) and a great tolerance to sound degradation during the decoding process are the keys to an optimal communication process.

Key words: acoustic communication, propagation-induced modifications, environmental constraints, evolution of communication.

INTRODUCTION

Communication, i.e. signal-based information transfer between individuals, supports social relationships in animals. In a classical view, a communication process can be described as follows: the signal, supporting information, is produced by an emitter and received by a receiver following propagation through a transmission channel. However, in most natural situations, animals belong to a communication network where any individual can act both as an emitter and a receiver at any time and where any information exchange between two interacting individuals can potentially be subject to eavesdropping by other members of the network (Dabelsteen 1992, McGregor and Dabelsteen 1996).

In songbirds, information transfer between individuals of communication networks plays an important role in both territorial conflicts and mate choice (Dabelsteen et al. 1998, Balsby and Dabelsteen 2003). Within forest environment, birds' networks are generally characterized by their relatively low population density: in most species males de-

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fend territories and are consequently situated far apart from each other – by several ten meters or even more – a situation that is very different compared for example with communication networks of colonial environments where the individuals are very near each other (e.g. Aubin 2004). Moreover, in the dense vegetation of forests, communication processes are constrained by propagation-induced modifications of the transmitted sounds (e.g. Wiley and Richards 1978, 1982). Indeed, the presence of tree leaves, trunks and branches induces important sound reverberation and absorption. This degradation leads to a diminution of the signal energy that may ultimately cause the signals to disappear in the background noise. Indeed, besides the spherical attenuation caused by the acoustic wave spreading away from the source on an increasing sphere (the energy in a given point of this sphere decreases approximately 6 decibels each time that the distance to the source doubles), absorption and multiple scattering caused by vegetation in the forest environment causes an excess attenuation. Transmitted signals are also qualitatively modified: amplitude modulations are rapidly altered, frequency-dependent attenuation changes the spectrum profile and may suppress high-pitched notes, and silences between notes are filled by echoes of reverberations (see Bradbury and Vehrencamp 1998 for a review). To stay effective, a signal has to be detected and discriminated by the receiver, which may be problematic since after some propagation distance the modifications of the signal structure can be so large that the receiver becomes unable to extract any pertinent information from it, for instance about the species identity of the sender. The ''active space'' of the sound signal depends on several factors. Some of them are imposed by the propagation channel (e.g. vegetation density, temperature, hygrometry, wind, vocalizations of other animals), while others are linked to intrinsic characteristics of the bird (intensity of the emitted signal, temporal and spectral features of the sound), and still others are controlled by the bird's behavior itself (e.g. perching and horizontal movements).

In forest environments, we thus deal with low-density networks where birds are located relatively far apart, combined with a highly reverberating and absorbing environment that causes high propagation-induced sound modifications. The aim of this paper is to briefly review the different strategies used by birds to manage with these constraints (see also Dabelsteen 2004).

EMITTER AND RECEIVER BEHAVIOR

Choice of a High Singing or Listening Post

Birds often sing from high perches referred to as song posts. Given that the forest environment is made of heterogeneous superposed layers of vegetation, active choice of sender and receiver positions may influence sound degradation and thereby the transmission range of emitted songs. Sound propagation experiments have shown that high perching of a signaler may counteract sound degradation and thereby increase the transmission range of their songs (Mathevon et al. 1996). However, perched birds also observe and listen to conspecifics and results from propagation experiments suggest that perching in a forest habitat may sometimes improve signal reception more than signal transmission (Dabelsteen et al. 1993, Holland et al. 1998). In these cases perching seems to result in more benefits when birds act as receivers than as senders. Maybe this is the main reason why some birds, e.g. the Wren *Troglodytes troglodytes*, perch in response to playback of propagation-degraded song (Mathevon and Aubin 1997, Holland et al. 2000).

Choice of the Time of the Day

The choice of the time of the day, or even the exact moment, to signal may also help a bird controlling the ''active space'' of its songs. It is well known that many birds show a diurnal pattern in their singing activity. One of the possible explanations is suggested by the ''transmission hypothesis'', which claims that birds sing most intensively at dawn because of reduced environmentally induced sound degradation at this time of the day. Indeed, some of the factors responsible for sound degradation are likely to vary over the day, for example, atmospheric turbulence, absorption, and level of abiotic background noise (Henwood and Fabrick 1979, Wiley and Richards 1982). Very few experimental studies have investigated this question. In a recent paper, Dabelsteen and Mathevon (2002) show that dawn conditions in a temperate deciduous forest do not always constitute the best circumstances for long-range communication. By performing a propagation experiment with song notes of the Blackcap *Sylvia atricapilla*, they showed that the background noise and the excess attenuation may indeed show a diurnal variation. In their experiment, which was made on a day almost without wind, excess attenuation decreased from dawn through the morning to early in the afternoon. The background noise was very high at dawn and early in the morning and conversely at its minimum level during the afternoon. Thus, the very high background noise generated at dawn and early in the morning by the simultaneous singing and calling of many different species of birds may constitute a good opportunity for communication that can be made private by the masking effect of the noise. More investigations dealing with this dawn chorus question are needed, and may be especially interesting in tropical environments where the meteorological conditions, unlike those in temperate climates, are constant over long periods.

CODING/DECODING PROCESSES

''Acoustic Adaptation Hypothesis''

According to the ''acoustic adaptation hypothesis'', the general structure of animal signals will differ depending on general features of the habitat (Morton 1975, Hansen 1979, Rothstein and Fleischer 1987). However, the support for this hypothesis is somewhat mixed. For instance, in a propagation study in a Neotropical rainforest, Nemeth and co-workers found a strong relationship between environmental conditions (height above the ground where the birds live) and the design of the vocalizations in three of the five antbird species they studied: song degradation in these three species ''was minimized by the concentration of the signal to a narrower frequency range, the usage of lower frequencies, or a slower time structure for the songs near the ground'' (Nemeth et al. 2001). For the two other species, there was no evident relationship between signal structure and propagation constraints. On a general point of view, the ''signal structure hypothesis'' suffers from many exceptions (Lemon et al. 1981, Rothstein and Fleischer 1987, Date and Lemon 1993, Fotheringham et al. 1997, Daniel and Blumstein 1998).

''Information Coding/Decoding Hypothesis''

Finally, the coding/decoding of information can be adapted to the propagation constraints. For instance, the information content of the song of both the Wren and the Blackcap rely on acoustic parameters that are resistant to propagation (Holland et al. 2000, Mathevon and Aubin 2001). Another example is the song of the Brazilian White-browed Warbler *Basileuterus leucoblepharus*. Its song, beginning with very high frequencies, is seriously altered during transmission through the tropical forest where the species lives (see Aubin et al. 2004). However, besides providing species information, this song allows the receiving bird to individually identify the singer, to range it, and perhaps to estimate its motivation (Aubin, Mathevon and Vielliard, unpubl. data). Each type of information is, or seems to be, encoded into particular acoustic parameters that differ in their ''active space''. Species identity is encoded into a parameter that resists sound degradation, whereas individual identity and perhaps also motivation are encoded into parameters more sensitive to propagation-induced modifications. Like in other species, cues for ranging are provided by the propagation-induced modifications.

CONCLUSION

The problems caused by environment with dense vegetation are different for the emitter and the receiver birds. From the emitter's point of view, the question is: how to reach the intended audience?

Indeed, propagation-induced constraints will reduce the active space of the emitted signals, i.e. the range over which the signal remains biologically significant for a receiver. The emitter's challenge is thus to control this range under the environmental pressure either to maximize the audience, e.g. in the case of a songbird attempting to attract females, or to restrict the audience to a particular receiver, e.g. during 'private' interactions with a mate. From the receiver's point of view, the problem is to optimize the acquisition of information from received sounds that are potentially seriously altered. Within an extreme acoustic environment, the discrimination of pertinent signals from the background noise, the decoding of information and the localization of the emitter can be especially challenging.

Adaptive strategies can be identified for both emitters and receivers (see also Dabelsteen 2004). From the emitter's point of view an adaptive strategy includes signaling behavior that takes into account both the physical heterogeneities of the forest environment and the temporal variations of the acoustic constraints in order to control the active space of signaling. The coding of information in acoustic parameters with varying susceptibility to propagation constraints is also important. To a receiver, adaptive behavior includes optimal choice of receiver post as well as a great tolerance to sound degradation during the decoding process.

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RESUMO

Na vegetação densa das florestas temperadas ou tropicais, os processos de comunicação são limitados pelas modificações dos sons durante sua propagação. A presença de folhas, troncos e galhos produz uma importante reverberação e absorção do som, provocando uma diminuição da energia do sinal, assim como modificações qualitativas. O objetivo deste artigo é de revisar brevemente as diferentes estratégias usadas por aves para gerenciar essas limitações. Para o emissor, um comportamento de emissão adaptado tanto às heterogeneidades físicas do meio florestal, quanto às variações temporais das exigências acústicas, é particularmente útil para controlar o canal ativo de sinalização. A codificação da informação em parâmetros acústicos com diferentes sensibilidades às exigências de propagação é também de grande valia. Para o receptor, um comportamento adaptado (posto de escuta) e uma ampla tolerância à degradação sonora durante o processo de decodificação são as chaves para um processo de comunicação otimizado.

Palavras-chave: comunicação acústica, modificações induzidas pela propagação, limitações ambientais, evolução da comunicação.

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