Bioacoustic diversity and resource partitioning in tropical calling communities

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Abstract. Several groups of tropical forest vertebrates and insects use acoustical signals for orientation and communication. Elevated sound levels due to "biotic noise" limit communication distance within highly diverse tropical lowland forests at Borneo and Northwest Amazonia. The ensemble of acoustically communicating animals is considered as an ecological community competing for acoustical transmission channels. Acoustical resource partitioning is achieved by diel periodicity and mutual inhibition of song activity. A subset of insects (Cicadidae and Grylloidea) engage in a dusk chorus showing exact on- and offset of song activity with an accuracy in the range of minutes 1. Mutual inhibition is observed among songsters singing on nearby frequencies, and such "jamming avoidance" occurs between different taxa, as f.e. katydids and frogs.

Key words. Bioacoustics, communication, diel periodicity, Borneo, Cicadidae, Ensifera, Anura.

Introduction

In tropical forests, a great number of animal species use acoustical signals for mate recognition and orientation. The high diversity of signals creates a complex acoustical environment with a high probability of signal interference. Therefore, one should expect resource partitioning of acoustic communication channels. Duellman & Pyles (1983) pioneered investigations on acoustical guilds by analyzing neotropical frog communities, Heller & von Helversen (1989) studied acoustical resource partitioning among bats, and quite a number of studies deal with sounds produced by tropical forest insects (Cicadidae: Pringle 1955, Duffels 1988; Gryllidoidea: Otte 1992, Riede 1993 a). All these studies concentrated on certain taxonomic groups. However, frequency range and even temporal structure of songs from completely distinct animals such as ensiferan Orthoptera and frogs overlap considerably, so that acoustical guilds cannot be delimited by taxonomic units. In this paper, calling communities from Bornean lowland forest are analyzed to

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1 Some of the cicada songs mentioned in the text can be heard via WorldWideWeb under: http://www.biologie.uni-freiburg.de/data/zoology/riede/cicada.html.

understand possible assembly rules and mutual influences between various taxonomic units.

**Study sites and methods**

Acoustical recordings in the audio-range (between 50 Hz and 20 kHz) where made during 7 months between 1991 and 1992 at Kinabalu National Park, Sabah, Malaysia, in a lowland mixed Dipterocarp forest at Poring Hot Springs (500 m asl). For further details, see Riede 1996.

**Results**

Figure 1 shows the considerable reduction of communication range within tropical rainforests due to "biotic noise" from other animals when compared with signals competing with quiet outdoor noise from temperate habitats. Such "abiotic noise" is generated by air turbulences or running water, and octave-band noise levels scale with frequency−1 (Fletcher 1992). In both habitats, signal intensity drops by spherical spreading and frequency-dependent attenuation losses (broken lines). The signal becomes undetectable when its intensity equals noise, i.e. at the intersection of noise bands with the respective signal attenuation curves (filled circles). The elevated noise levels within the forest reduce the communication range considerably (open squares). Besides overall intensity increase, forest noise bands do not drop with frequency−1, but are elevated due to "biotic noise" from singing animals, and possibly by vegetation noise from dry rustling leaves (especially around 20 kHz). These theoretical considerations delimit maximal communication ranges without taking into account the receptor physiology of the receivers or the specific properties of animal sounds contributing to "biotic noise".

Noise levels increase around 15 dB(A) at dusk, mainly due to certain Cicadidae and Gryllotalpidae (Riede 1996). Species engaging in the dusk chorus are all characterized by very loud songs, and therefore easy to record and analyze (Gogala & Riede, 1995). Their song activity is limited to dusk, and even within this small time window, temporal segregation can be observed (Figure 2). The precision of entry and short overall calling time leads to a complete uncoupling of calling activity between species, and therefore is an efficient way to reduce acoustic interference. Temporal segregation is much more pronounced among the dusk community than among cicadas singing during daytime. With the exception of one species (*Dundubia vaginata*), there is no overlap between the diurnal and dusk community of singing cicadidae. Though calling activity of diurnally singing cicada species extends in the range of hours (Riede & Kroker, 1995), sound levels generated by diurnal calling communities never reach the intensity and complexity of the dusk chorus. Temporal segregation seems to be substituted by spatial segregation: dusk species have large and continuous geographic distributions, while
Figure 1: Communication distance for a sound source of 0.1 mW (equal to human speech, bird song) at various frequencies (broken curves: attenuation with frequency as a parameter) in the presence of typical outdoor octave-band noise levels at the same frequencies (about 30 dB(A) overall, broken lines at the right half, after Fletcher 1992, p. 282), and in the presence of noise from Bornean rainforest (about 47 dB(A) overall, measured 20 m above ground in lower montane mixed dipterocarp forest, 11.4.1994, 17:45, Poring, Sabah). The intersections of signal and noise curves define the maximum distance beyond which the respective frequencies cannot be differentiated, i.e. the maximum communication distance (solid lines with full circles for signal vs. outdoor noise, stippled line with squares for signal vs. forest noise). Note that communication distance within rainforest is considerably lowered because of elevated overall sound level, mainly due to "biotic noise" from singing animals. Note that the 20 kHz octave band coincides with 1kHz band at 52 dB. Further explanations see text.

diurnal species show much higher local diversity, i.e. only few species can be found at one locality. Consequently, their overall regional diversity is higher than that of the dusk species.

The following examples deal with direct interference of songsters, which might result in complete suppression of calling activity: as shown in Figure 2, crickets start only after the termination of the loud cicada dusk chorus. Crickets start earlier at dusk in Northwest Amazonia, where the dusk chorus is not dominated by Cicadidae (Riede 1993 a).

Further evidence for mutual inhibition is observed among songsters singing on nearby frequencies. Their "jamming avoidance" results in alternating chirps, for
example between the pseudophylline Tettigoniid *Tympanophyllum* spp. and frogs (*Metaphrynella sundana*), both singing on nearby frequencies between 1 and 2 kHz (Riede 1993 b).

**Discussion**

Acoustical communication range within tropical forest is reduced considerably by elevated biotic noise bands. In addition, physiological mechanisms such as masking...
by nearby frequencies further reduce signal detection in vertebrates and possibly insect ears. Efficient means of acoustic transmission channel partitioning are temporal segregation and "jamming avoidance." Especially at dusk, there is strong competition for transmission channels among several loud-singing species. Their temporal segregation described above is mediated by species-specific tuning to a narrow signalling time window. Temporal segregation minimizes acoustic interference, and the necessary precision of timing at dusk could be achieved by external triggering factors such as fading light intensity or changes in spectral composition. In contrast, diurnally signalling species show much broader time windows of signalling activity. However, acoustical interference is not critical due to pronounced spatial segregation of these species.

A further mechanism to minimize signal interference is "jamming avoidance" by mutual inhibition of songsters. Such interactions can occur between distinct systematic units signalling on overlapping frequency bands, e.g. katydids and frogs. Therefore, an analysis of assembly rules for "acoustical guilds" has to include all systematic units showing acoustic communication.

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References


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