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14 Partitioning of Acoustic Transmission Channels in Grasshopper Communities

Maria Bukhvalova

Most works on bioacoustics of insects have been concerned with signals and the structure of the communication system, either in a single species or in groups of closely related ones. Investigations of acoustic interactions between sympatric species dwelling in the same biotope are scarce. Still, information on the subject is available both for groups of sympatric species belonging to the same taxonomic unit, *e.g.* singing cicadas, and for communities of sound-producing animals as a whole.

Wolda (1993) described interspecific acoustic interference for singing cicadas (Cicadidae) in Panama. The breeding seasons of two of three sympatric species forming a “dusk chorus” completely overlap. The season of acoustic activity of the third species began only a day or two after the last singing male of one of the first two species had disappeared. Two other species, *Selymbrya achyettios* Ramos and *Pacarina puella* Davis, also differ in breeding seasons when they are sympatric (approximately December to February and March to April, respectively). In a locality where *P. puella* alone was present, it was found during the longer period from December to April. It is quite possible that the reason for the shifting of singing season of this species was acoustic interference with *S. achyettios*.

Acoustic segregation between different higher taxa also takes place. Investigators in a Bornean lowland rain forest showed that they were able to attribute most songs accurately either to vertebrates (mammals, birds and frogs) or to different insect groups (crickets, katydids and cicadas), even when the singer was not visible. This was possible because each such group had its own “acoustic appearance” (Riede, 1996). Acoustic activity of singing cicadas in the studied area was diurnal while crickets started singing at dusk, followed by the strictly nocturnal katydids. Thus, there is a pronounced temporal segregation between these taxa.

The situation observed in other groups of animals is more or less similar. Thus, among 15 Central Amazonian sympatric species of frogs breeding synchronously on the mats of floating vegetation, 14 produced mating calls differing distinctly from each other in dominant frequency and temporal pattern. Two species with similar calls demonstrate spatial segregation of calling sites. One of these calls from the peripheral parts of floating meadows at water level among aquatic plants distributed low over the water surface. The other perches on high grass growing nearer to the edge of a flooded forest (Hödl, 1977).

Thus, competition and niche segregation between species in ecological communities involve not only territory, food and other similar resources, but also acoustic transmission channels. Partitioning of communication channels in grasshopper assemblages will be discussed here.

In the Palearctic region, Gomphocerine grasshoppers are diverse and numerous in meadows, glades and other open habitats. Generally, all Gomphocerinae are active during the daytime, so one can hear signals of about ten species singing simultaneously in the same biotope and sounding like an unceasing chorus to the human ear. The structure of such a chorus is one subject of the author’s study.

It is evident that calling signals of each species must differ in at least one physical parameter from signals of all other sympatric simultaneously singing ones. Otherwise, recognition of a conspecific signal by a potential mate would be impossible. Signals of Gomphocerinae have wide-band noise frequency spectra, widely overlapping in different species. There is no evidence of use of frequency characteristics for recognition of conspecific songs in these insects (Meyer and Elsner, 1997). For this reason, only temporal pattern in the comparative analysis of signals in assemblages of grasshoppers will be considered here.

The temporal pattern of Gomphocerine signals is very elaborate and diverse. Still, from a collection of oscillograms of songs of sufficient species, it can be seen that certain signals are very similar in general structure and in temporal pattern of syllables. As a result, most of the song patterns fall into one of a small number of basic categories. The classification and terminology of signals used in this chapter is similar to that of Ragge and Reynolds (1998), but it covers Gomphocerine grasshoppers only. Calling signals of Gomphocerinae consist either: (1) of single (or repeated, but with irregular pauses) echeme or (2) of those repeated with regular intervals (echeme-sequence, according to Ragge and Reynolds, 1998) (Figure 14.1). In (2), the song may last for a minute or more. In (1), normally producing single echemes, a similar situation may arise very occasionally in males with unusually high acoustic activity. In several species normal song as a rule consists of a sequence including two or three echemes, as in *Chorthippus biguttulus* L. and *Ch. maritimus* Mistsh. (Figure 14.4). Nevertheless, they frequently produce single echemes. On the other hand, songs with more than three to four echemes are very rare. For this reason we attribute such signals to category (1) of single or irregularly repeated echemes.

Within each category two major groups may be separated. In the signals belonging to the first group (1), each syllable consists of a rather prolonged low-amplitude initial part and several shorter high-amplitude fragments separated by distinct gaps. Species producing single echemes (2) are numerous, including *Stenobothrus stigmaticus* Ramb., *S. fischeri* Eversmann and *Ch. vagans* Eversmann (Figure 14.4). Syllables in the songs of *Ch. parallelus* Zett. (Figure 14.4), *Ch. montanus*

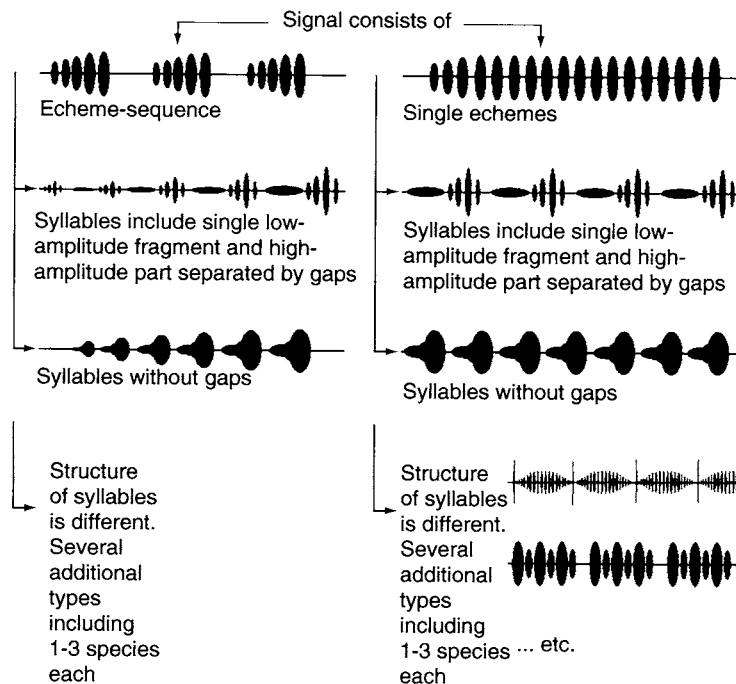


FIGURE 14.1 Classification of songs of Gomphocerine grasshoppers based on characters of temporal pattern.

Chorp. (Figure 14.2), *Euchorthippus* species (Figure 14.4) and in a number of other species have the same structure, but the signal is an echeme-sequence.

The second group includes signals consisting of syllables without distinct gaps. Only in certain cases are low- and high-amplitude parts of the syllable separated by low-amplitude gaps. Single echemes consisting of such continuous syllables are intrinsic to *Omocestus viridulus* L., *O. haemorrhoidalis* Ch. (Figure 14.2), etc. *Chrysochraon dispar* Germ., *Euthystira brachyptera* Ocsk., *Stenobothrus nigromaculatus* H.-S. and a few other species produce echeme-sequences with the same syllable pattern.

As a result, four main types of signals may be separated. In addition, in a number of species the structure of syllables is quite different. For such species, several additional types, usually including one to three species each, may be recognised. The number of such “nontypical” species is not great, however. Among signals of more than 70 species of West European grasshoppers described by Ragge and Reynolds (1998), about 60% can be attributed to one of the four main types. Similarly, 24 of 35 species from Russia and adjacent territories (about 65%) produce signals belonging to one or another of these types (Bukhvalova and Vedenina, 1998; Vedenina and Bukhvalova, 2001).

It should be noted that the only purpose of this classification is to reveal the characters by which the signals of sympatric species differ from each other. It does not display phylogenetic relationships. Moreover, occasionally species from different genera produce quite similar songs, whereas closely related ones differ distinctly in temporal patterns.

Eleven grasshoppers assemblages in the Moscow Area, the steppe zone of the Lower Volga Region, the mountains of Northern Caucasus (Ossetia), Southern Siberia (Tuva) and the Russian Far East (Khabarovsk Province) were studied. In each community, signals of sympatric species were analysed and classified according to the scheme described above (Figure 14.1). All recordings were made at a shade air temperature of 26 to 31°C. Differences between the signals belonging to different types are obvious. Reliable characters for discrimination between the signals of different species within the same type are not so easy to find.

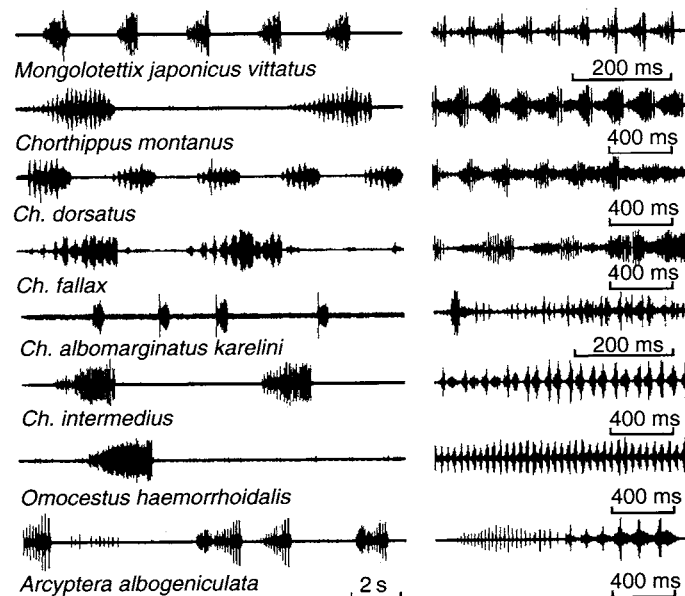


FIGURE 14.2 Oscillograms of calling songs of Gomphocerinae from a grasshopper assemblage in the floodland of Tes-Khem River in Southern Tuva (Southern Siberia). Two oscillograms of each signal are given at different speeds.

Echeme duration, as well as the echeme repetition period in species producing echeme-sequences, are variable and may overlap widely in sympatric species. The number of gaps (if present) in a syllable is also a variable character. Moreover, in certain species with similar patterns of syllables, the number of gaps is the same.

Comparison of the syllable repetition period (SRP) in signals belonging to the same type showed that the songs of sympatric species differ distinctly in this feature. This appeared to be quite similar in all biotopes studied. For this reason only one typical example will be described here, namely, the community of eight sympatric species in the floodland of Tes-Khem River in Southern Tuva (Southern Siberia) (Figure 14.2 and Figure 14.3).

The signals are subdivided into groups according to the classification given above (Figure 14.3). Species producing single echemes consisting of syllables with gaps, as well as species producing songs of any additional types, were absent from this community. The real distributions of values of SRP for each species are represented as a histogram. The following are general rules that appear to be observed in all communities. First, signals within the same type always have different SRP, only slightly overlapping in edge values. Second, the SRP in signals belonging to different types can overlap almost entirely. Only occasionally did we not find significant differences, for example in *Mongolotettix japonicus vittatus* Uvarov and in the second part of signal of *Arcyptera albogeniculata* Ikonn.

When the signal consists of two different parts, the situation is more complicated. Thus, in *A. albogeniculata*, the signal includes two successions of syllables (Figure 14.2). Sometimes these follow each other without a break forming a unified song. In other examples the two parts are subdivided by a pause lasting up to several seconds. Occasionally, a male omits any of the parts and the reduced signal consists of only one sequence of syllables. As a result, two sequences of syllables occasionally sound like different signals not connected to each other. In SRP these parts do not overlap either with each other or with signals of other species (Figure 14.3).

In *Chorthippus dorsatus* Zett., the first (main) part of the signal has a typical temporal pattern (Figure 14.2), whereas the second one is a monotonous fragment with indistinct inner structure. By contrast, in *A. albogeniculata* the pattern of song is constant and the second part is a necessary component of each signal. The SRP in the first part of the signal of *Ch. dorsatus* completely overlaps with that of *Ch. montanus* (Figure 14.3). Syllables in these two species also have the same

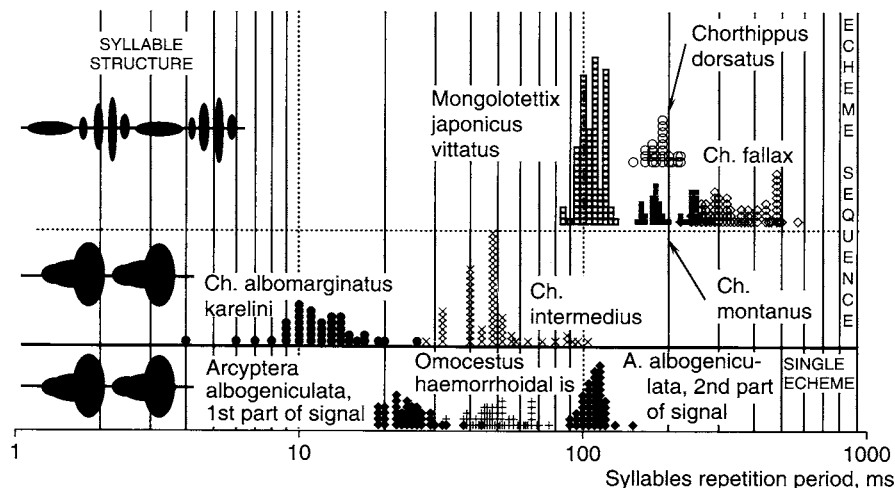


FIGURE 14.3 Histograms of distribution of syllable repetition period in eight sympatric species of Gomphocerinae from a grasshopper assemblage in the floodland of Tes-Khem River in Southern Tuva (Southern Siberia). Time scale is logarithmic.

pattern (Figure 14.2). Apparently, the song of *Ch. dorsatus* is exceptional among similar signals of sympatric species in the presence of additional fragments. The same phenomenon has been observed in a grasshopper community in the Moscow Area where this species coexists with *Ch. parallelus*, having almost the same SRP (for oscillogram of signal of the latter, see Figure 14.4).

Species producing signals of the same type with the same SRP were never found to be sympatric. For example, signals of *Ch. vagans* and *Ch. macrocerus* Fischer-Waldheim belong to the same type, namely, single echemes consisting of syllables with gaps (Figure 14.4). The SRP in both species are similar. According to our observations in the Lower Volga Region (Rostov Area), these species can live in the same locality, but they always inhabit different biotopes. *Ch. macrocerus* was found in steppes and other open habitats (on roadsides among the fields, etc.), but *Ch. vagans* lived exclusively in glades in forest plantations and on the edges of forest shelter belts. Thus, the two species replaced each other in different communities, whereas the remaining species producing signals of this type remained the same (Figure 14.5).

Several other examples of mutual replacement also were observed in the steppe zone of European Russia. *Ch. parallelus* was found here in all open habitats, but on saline land near Volgograd, it was replaced by *Eremippus costatus* Tarb., dwelling in the thickets of *Artemisia* (*Seriphidium*) (Figure 14.6). Signals of both species have the same type of temporal pattern and similar SRP (Figure 14.4).

Signals of *Ch. macrocerus* and *Stenobothrus miramae* Dirsh are also very similar, both in temporal structure and quantitative parameters (Figure 14.4). *S. miramae* was found in the Crimea, in steppes and anthropogenic landscapes, and also in the steppes of the Orenburg Region (South Urals). However, it was not found elsewhere in the steppe zone of south-east European Russia (between Crimea and South Urals). At the same time, in all localities studied in this area, *Ch. macrocerus* was present. Both species have very wide ranges of environmental tolerance. Two places where *S. miramae* was found are quite different in climatic conditions. The range of *Ch. macrocerus* includes central and southern parts of European Russia (northwards as far as Kursk), Caucasus (in Ossetia we have found this species both in the plains and on subalpine meadows about 2000 m above sea level), Transcaucasia, Northern and Western Kazakhstan,

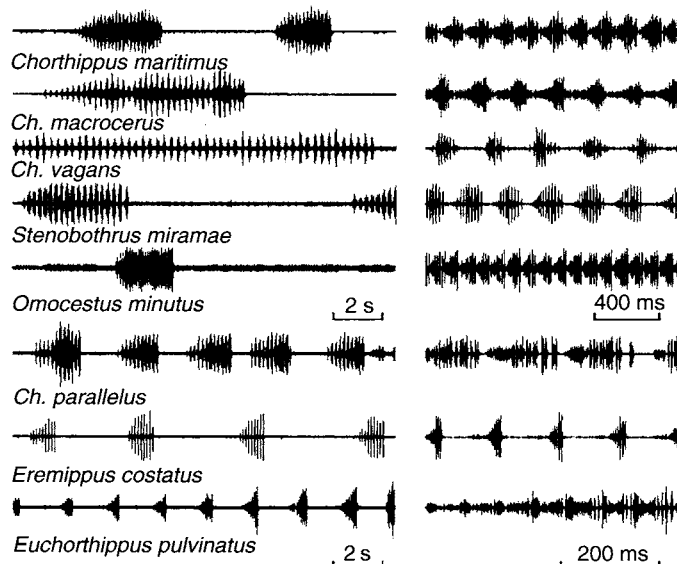


FIGURE 14.4 Oscillograms of calling songs of Gomphocerinae from steppe zone of European Russia. Two oscillograms of each signal are given at different speeds.

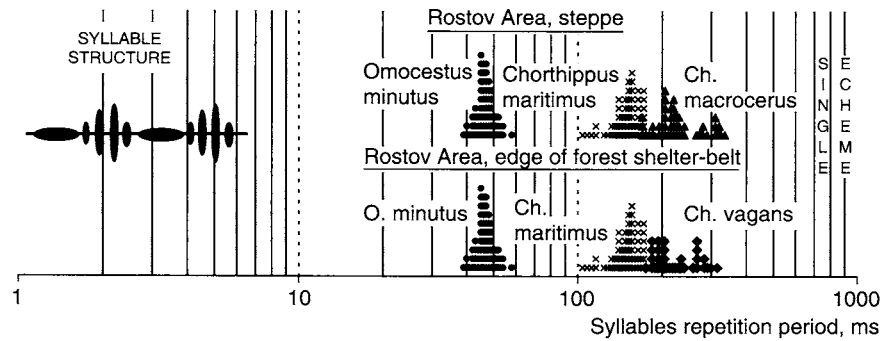


FIGURE 14.5 Histograms of distribution of syllable repetition period in four species of Gomphocerinae producing single echemes consisting of syllables with gaps. Time scale is logarithmic.

Turkmenistan (Kopet-Dagh Mountains), Iran and Afghanistan. It may be that the reasons for the allopatry of these species do not lie in a difference in ecological conditions between localities, but in the similarity of their calling signals.

Thus, we can note the third general rule observed in grasshoppers communities. The free range of SRP can be occupied in different communities by different species, but the place of this range on the time scale remains unchanged. The probable explanation of this phenomenon may be as follows. Difference in species composition between communities in different biotopes or localities is not great. As a rule, one can observe the appearance and loss of a small number of species in every biotope in comparison with nearby ones. For this reason, every species appearing in the community can occupy only the free range on the SRP scale of its signal. Consequently, in different biotopes and localities, species composition varies to some extent but the ranges of SRP that can be occupied by the signals remain the same.

As a result, all the complex of temporal parameters of the signal, including the general structure (single echemes or echeme-sequence), temporal pattern of syllables and the range of SRP determine for the song of each species its own "place" in the acoustic environment of the community, so-called acoustic niche, which is a part of the ecological niche as a whole (Zhantiev, 1981). Acoustic niche may be defined as the range of acoustic parameters of environment in which successful communication of the species is possible.

It can be assumed that the above-mentioned characters are most important for recognition of conspecific signals in Gomphocerinae. Ethological experiments with retranslation of model songs

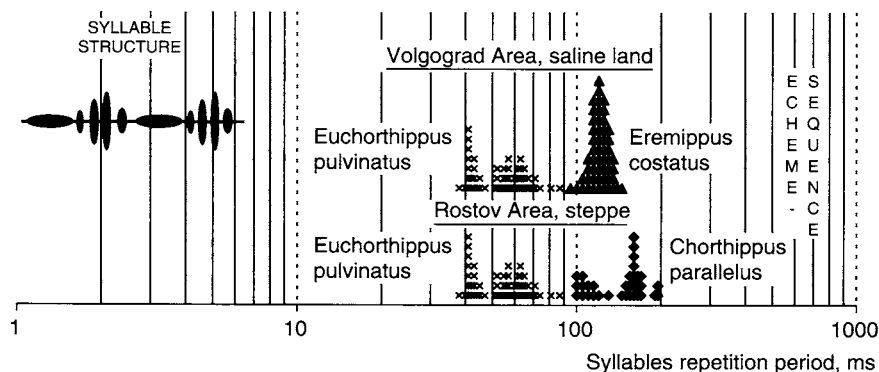


FIGURE 14.6 Histograms of distribution of syllable repetition period in three species of Gomphocerinae producing echeme-sequences consisting of syllables with gaps. Time scale is logarithmic.

to receptive females corroborate this supposition. Females of *Ch. biguttulus*, *Ch. parallelus* and *Ch. dorsatus* demonstrated significantly more higher levels of response reactions to artificial signals with gaps than to ones without gaps (Vedenina and Zhantiev, 1990; von Helversen and von Helversen, 1998). Apparently, the insects are capable of distinguishing between the two types of syllable patterns. As demonstrated in recognition tests on *Ch. biguttulus* (von Helversen and von Helversen, 1998), *Ch. parallelus* (Dagley *et al.*, 1994) and *O. viridulus* (Eiriksson, 1993), SRP also plays substantial role in the identification of conspecific song.

As a whole, the results of the comparative investigation of calling signals in grasshopper communities demonstrate that acoustic environment is at least as important for Gomphocerinae as other ecological conditions. For this reason, competition between species is not only for food and territory, but also for acoustic transmission channels. Sometimes, the absence of a free channel appears to be the main factor limiting the distribution of species and determining the species composition of the community.