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Background noises in vibratory communication channels of Homoptera (Cicadinea and Psyllinea)

Помехи в каналах вибрационной коммуникации равнокрылых (Cicadinea и Psyllinea)

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KEY WORDS: Homoptera, Psyllinea, Cicadinea, Auchenorrhyncha, vibratory signals, vibratory communication, background noises.

КЛЮЧЕВЫЕ СЛОВА: Homoptera, Psyllinea, Cicadinea, Auchenorrhyncha, вибрационные сигналы, вибрационная коммуникация, помехи.

ABSTRACT. Vibrations induced in plant stems by wind and mechanical activity of insects are investigated. The most of the energy of vibrations is concentrated in the range up to 1 kHz, usually additional peak at the frequencies from 2 to 4 kHz presents in the frequency spectrum. If the amplitude of vibrations is rather low, vibratory signals of Homoptera (Cicadinea and Psyllinea) can be distinguished against background noises. When the wind velocity is high, noises can jam the signal and communication became impossible. Possible ways to avoid wind-induced noises are discussed. It is demonstrated, that in certain cases insects do not sing if the amplitude of noises is high, but produce their signals only during the periods of lull between the wind rushes.

РЕЗЮМЕ. Зарегистрированы вибрации, возникающие в стеблях растений при ветре и механической активности насекомых. Основная энергия колебаний сосредоточена в диапазоне до 1 кГц; как правило, в частотном спектре присутствует дополнительный пик на частотах от 2 до 4 кГц. Если подобные помехи имеют сравнительно невысокую амплитуду, вибрационные сигналы равнокрылых (цикадовых и листоблошек) вполне различимы на их фоне. При сильном ветре сигнал может быть полностью заглушен помехами, и коммуникация становится невозможной. Рассмотрены возможные способы избегания помех в подобной ситуации. Показано, что в некоторых случаях насекомые не поют при наличии сильных помех, издавая сигналы только в периоды затишья между порывами ветра.

For a long time insects producing airborne sounds, such as crickets, katydids (Orthoptera) or singing cicadas (Cicadidae) remained the main objects of bioacoustics of insects. Until now the main body of information on the subject concerns representatives of these two taxa. The number of works on vibratory communication of insects increased considerably only in last two decades. Presently, the fact that communication by means of substrate-borne vibrations is prevalent in insects became generally accepted [Cocroft & Rodríguez, 2005].

Recording of low-amplitude vibrations in plant stems and leaves requires rather sophisticated and cumbersome equipment. For this reason, investigation of vibratory signals of insects is almost exclusively laboratory-based field of research. For one thing, laboratory conditions easily allow to obtain recordings of good quality, for another, in this situation researcher remains quite unaware of various kinds of background noises which can interfere with communication signals of insects under investigation.

At present, vibratory signals of about 450 species of small Homoptera (Psyllinea and Cicadinea excluding Cicadidae) are described in literature. Only several attempts of field recording of signals of these insects were undertaken, however. Claridge and Morgan [1989] have made field recordings of signals of *Hindola* sp. (Machaerotidae) in Indonesia. Field studies of social behaviour and acoustic communication in several species of treehoppers (Membracidae) were conducted by Cocroft [1999, 2003]. Similar works on representatives of other invertebrates are also rare; references concerning this subject can be found in Cockroft and Rodríguez [2005].

The aim of the present work is to reveal various sources of background noises, which can affect vibratory communication of Homoptera (Cicadinea and Psyl-

linea), and to study certain physical characteristics of the noises.

Cocroft and Rodríguez [2005] list the following possible sources of vibratory noises: wind, rain, movements and acoustic activity of other insects, and airborne sounds inducing vibrations in plant stems.

In European Russia where our investigations were conducted, the main part of precipitation falls on the cold season. Moreover, in the summer, rain as a rule is accompanied by lowering of air temperature, which results in decreasing of insect activity. Thus, noises produced by falling raindrops hardly have any substantial effect on insect communication in our climate. Nonetheless, in tropical rain forests it can appear to be the major contributor of background noises.

Certainly, airborne sounds can induce vibratory noises in plant stems. However, piezo-electric crystal vibrotransducers such as gramophone cartridges or accelerometers are not suitable for their investigation, because they sense sound waves directly as well. This feature can be used for expeditious recording of remarks and comments without resort to microphone during experiments with registration of insect vibrational signals.

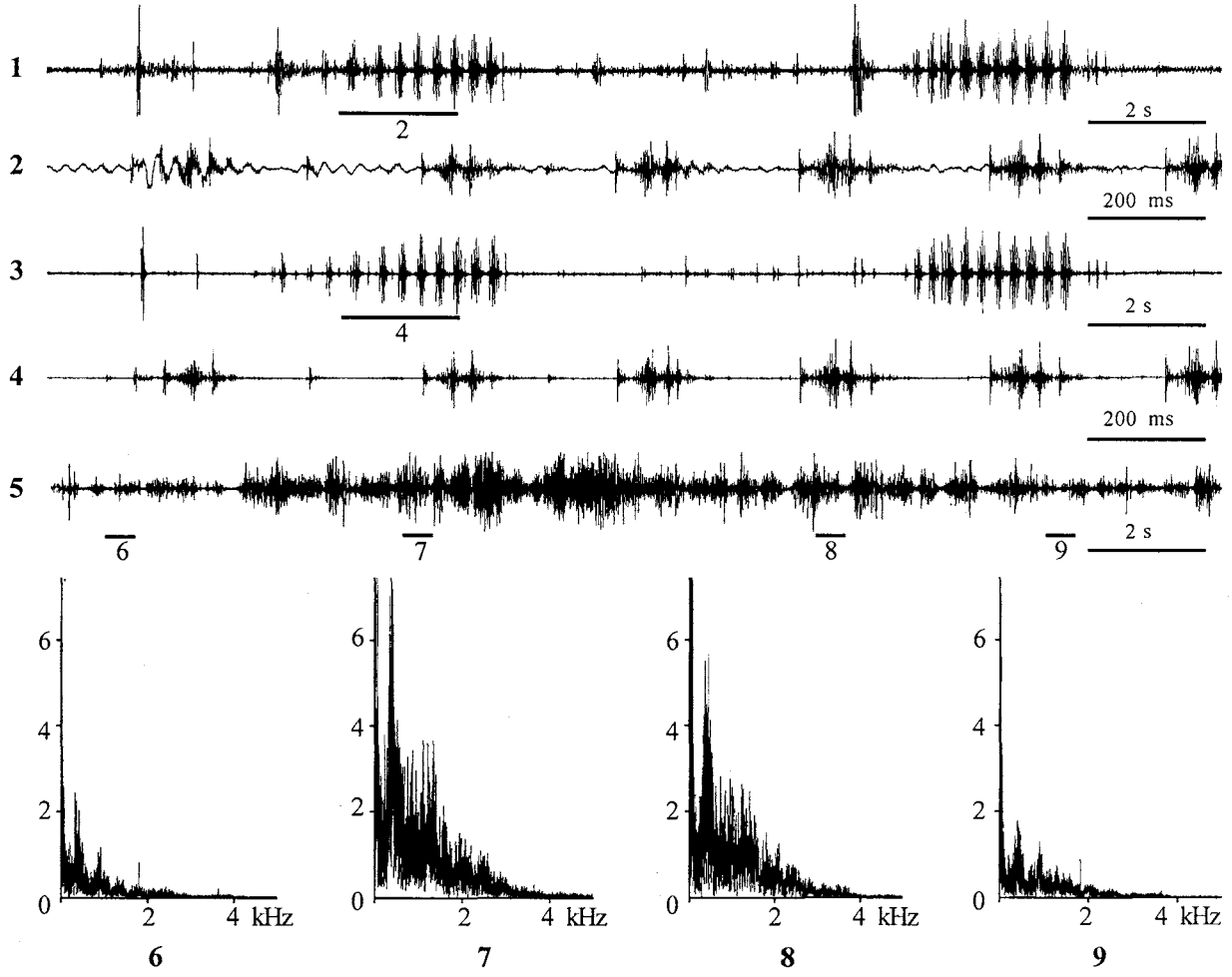
Three remaining kinds of sources of noises, i.e. wind, movements of insects, and their vibratory signals to be considered below.

All recordings of vibratory signals and noises were made in nature by means of piezo-electric crystal gramo-

Table. Plant and insect species studied and conditions during recording of vibratory signals and noises
Таблица. Изученные виды растений и насекомых и условия во время записи вибрационных сигналов и шумов

No.	Plant	Conditions of growth and height of a stem	Maximal amplitude of wind-induced movements of the tip, cm	Insect	Recording site	Temperature during recording of signals of insects, °C
1	*Cytisus ruthenicus* Fisch. ex. Woloszczak (Fabaceae)	Single plant about 1 m high	15	*Gargara genistae* (F.) (Membracidae)	Saratov Area, Krasnokutskiy Reg., env. Dyakovka Village.	34
2	*Bolboschoenus maritimus* (L.) Palla (Cyperaceae)	Thickets with average height 60–70 cm, stems touch each other	4–5	*Aglena ornata* (H.-S.) (Cicadellidae)		—"—
3	*Artemisia absinthium* L. (Asteraceae)	Single stem about 1 m in length half-laying in the grass	2–3	None	Moscow Area, Voskresensk Distr., env. Beloozerskiy Town	
4	—"—	Single stem 70 cm high standing upright	10	None		
5	*Populus tremula* L. (Salicaceae)	Young tree 50 cm high	3 *	None		
6	*Calamagrostis epigeios* (L.) Roth (Poaceae)	Single stem 35 cm high not touching other stems	1–2	*Javesella dubia* (Kbm.) (Delphacidae)	Moscow Area, Serpukhov Distr., env. Luzhki Village	25–27
7	—"—	—"—	—"—	*Criomorphus albomarginatus* (Curtis) (Delphacidae)		—"—
8	Undetermined grass species (Poaceae)	Thickets with average height 20–25 cm, stems touch each other	2–3	—"—		—"—
9	*Achillea millefolium* L. (Asteraceae)	Single plant 20 cm high	0.5	*Craspedolepta nervosa* (Först.) (Aphalaridae)	Moscow Area, Voskresensk Distr., env. Beloozerskiy Town	34
10	—"—	—"—	—"—	*C. nervosa* and *Graphocraerus ventralis* (Fall.) (Cicadellidae)		—"—

* also, all leaves tremble.



Figs 1–9. 1–4 — oscillograms of calling signals of *Javesella dubia* (No.6 in the Table): 1–2 — non-filtered signal; 3–4 — same, frequencies up to 200 Hz are rejected; 5 — oscillogram of wind-induced vibrations in the stem of *Cytisus ruthenicus* (No.1 in the Table); 6–9 — same, frequency spectra of different parts of the recording. Parts of signals indicated as 2, 4, 6–9 are given on oscillograms and spectrograms under the same numbers. Y-axis of spectrograms is graduated in per-unit notation.

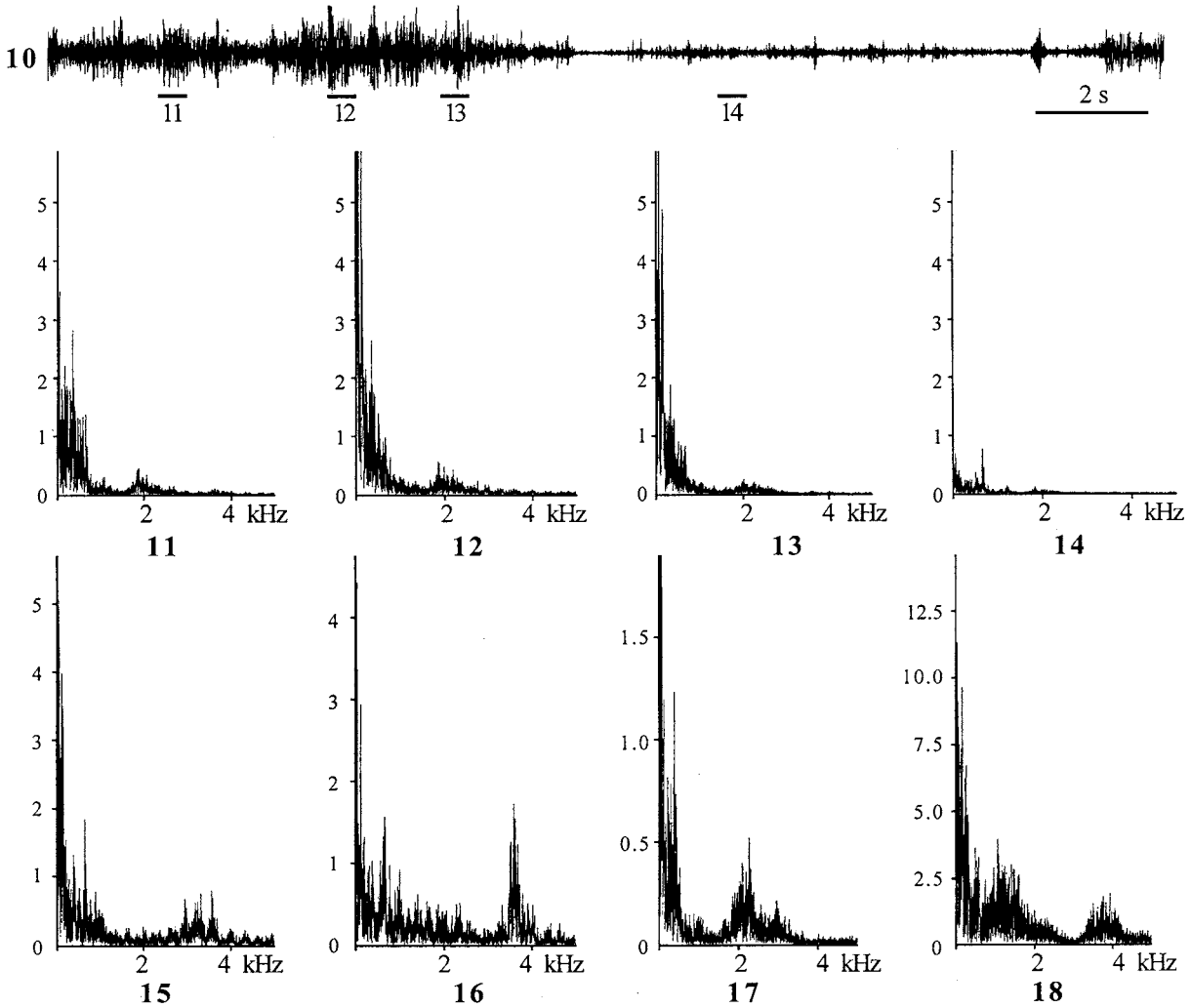
Рис. 1–9. 1–4 — осциллограммы призывных сигналов *Javesella dubia* (№ 6 в таблице): 1–2 — нефильтрованный сигнал; 3–4 — то же, отфильтрованы частоты до 200 Гц; 5 — осциллограмма вызванных ветром колебаний в стебле *Cytisus ruthenicus* (№ 1 в таблице); 6–9 — то же, частотные спектры разных частей записи. Фрагменты сигналов, обозначенные цифрами 2, 4 и 6–9 представлены на осциллограммах и спектрограммах под такими же номерами. Масштаб по оси Y на спектрограммах — в условных единицах.

phone cartridge connected to the microphone input of cassette recorder "Elektronika-302-1" or minidisk recorder Sony Walkman MZ-RH910 via the matching amplifier. In all cases manual mode of recording level control was used. Cartridge was attached to the stem near the root and laid freely on the ground. Thus, the effect of additional mass fixed on the plant was minimized.

Insects were collected immediately before the experiment in the same biotope, where the recording was made. They were put on the stem to which the equipment has been connected. A number of individuals escaped, but certain ones remained on the stem and as a rule started singing in a few minutes. In one case, during recording of signals of *Craspedolepta nervosa* (Först., 1848), the male of *Graphocraerus ventralis* (Fall., 1806) have jumped on the stem and produced calling song. Thus, the recording of two simultaneously singing species was obtained (No.10 in the Table).

There is no close relation between amplitude of movements of leaves or stems and average wind velocity measured by anemometer. First, wind velocity is extremely variable: usually, short rushes of wind alter with periods of lull. Second, even in the plain, local wind velocity in little hollows, under the bushes or trees and in other sheltered places can differ much from this in the open area. Moreover, in certain cases the intensity of vibratory noises depends not only on the wind velocity, but also on the properties of the plant itself; trembling poplar (*Populus tremula* L.) is a prominent example. For this reason, we measured not wind velocity, but the length of the stem and amplitude of movements of its tip. Data on plant and insect species studied and conditions during recording of vibratory signals and noises are given in the Table.

Recording equipment was not calibrated. For this reason, Y-axis of spectrograms is graduated in per-unit



Figs 10–18. 10 — oscillogram of wind-induced vibrations in the stem of *Artemisia absinthium* (No.3 in the Table); 11–14 — same, frequency spectra of different parts of the recording; 15 — frequency spectrum of wind-induced vibrations in the stem of *A. absinthium* (No.4 in the Table); 16 — same, *Populus tremula* (No.5 in the Table); 17 — same, *Achillea millefolium* (No.9 in the Table); 18 — same, *Bolboschoenus maritimus* (No.2 in the Table). Parts of signals indicated as 11–14 are given on oscillograms and spectrograms under the same numbers. Y-axis of spectrograms is graduated in per-unit notation.

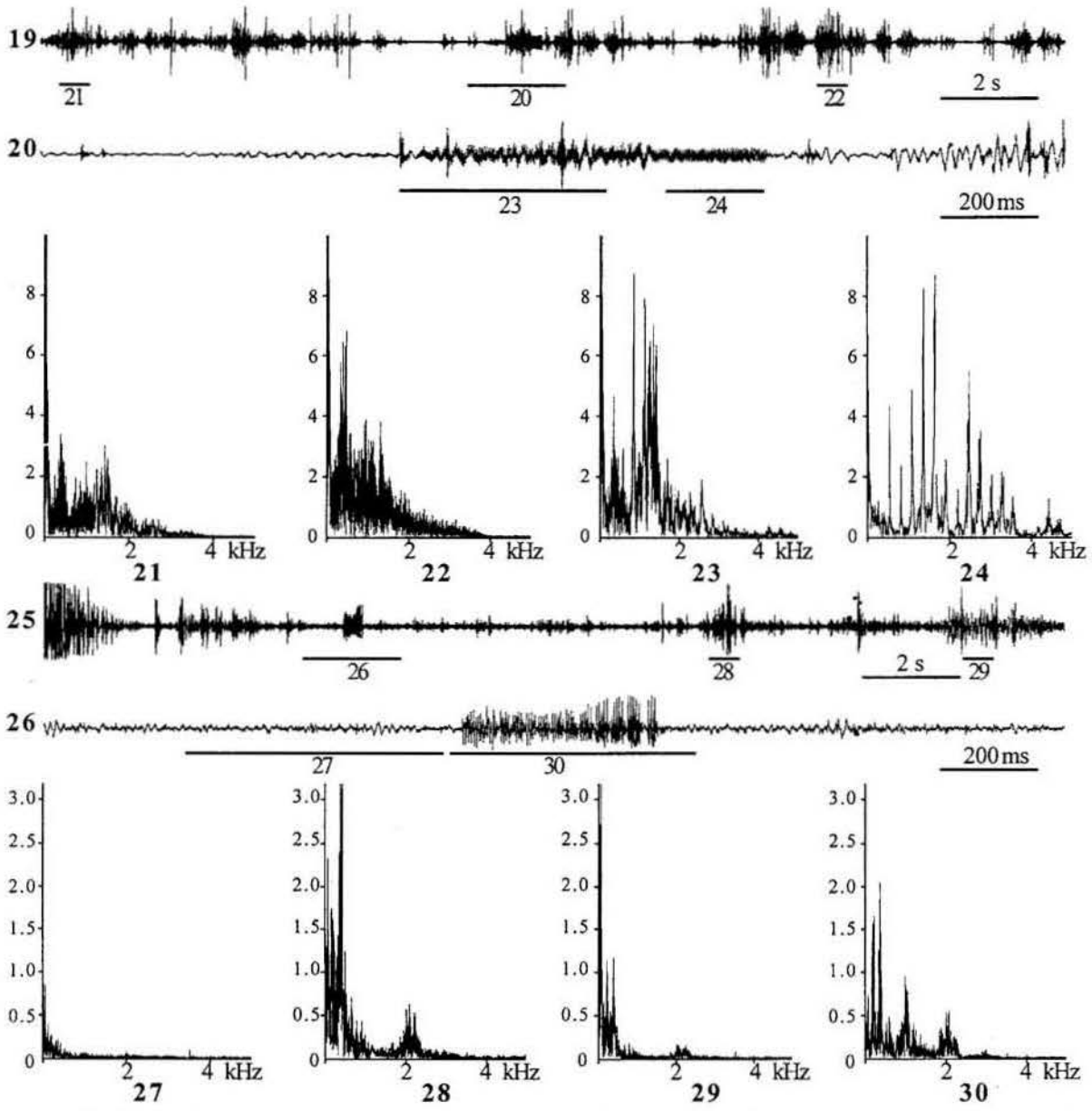
Рис. 10–18. 10 — осциллограмма вызванных ветром колебаний в стебле *Artemisia absinthium* (№ 3 в таблице); 11–14 — то же, частотные спектры разных частей записи; 15 — частотный спектр вызванных ветром колебаний в стебле *A. absinthium* (№ 4 в таблице); 16 — то же, *Populus tremula* (№ 5 в таблице); 17 — то же, *Achillea millefolium* (№ 9 в таблице); 18 — то же, *Bolboschoenus maritimus* (№ 2 в таблице). Фрагменты сигналов, обозначенные цифрами 11–14, представлены на осциллограммах и спектрограммах под такими же номерами. Масштаб по оси Y на спектрограммах — в условных единицах.

notation. This allows comparing the amplitude of signal in different parts within the same recording, but not between different recordings. The amplitude of signals varied greatly from one experiment to another, so it was impossible to set the same recording level in all cases.

Wind appeared to be the main source of vibratory noises in the region of our investigations. If the weather is more or less still, clear recordings not differing from these made under laboratory conditions can be obtained easily (Figs 1–4).

Local wind velocity and, consequently, amplitude of vibratory noises induced in the plant stems can change greatly and abruptly several times even over the course of several seconds (Figs 5, 10). Frequency spectra of different parts of recording made on the same plant under such conditions are quite similar, however (Figs 6–9, 11–14). On the other hand, differences between spectra of noises in different stems or twigs are rather well pronounced (Figs 15–18). Thus, it may be concluded, that these are physical properties of the individual stem, which determine the appearance of the frequency spectrum, whereas wind velocity affects mainly the amplitude of vibrations (Figs 6–9, 11–14).

Generally, frequency spectra of wind-induced vibrations in different plants are similar. Main energy of noises is concentrated in the range up to 1–2 kHz and abruptly decreases with increasing frequency. Usually, additional peak of lesser amplitude between 2 and 4 kHz presents (Figs 15–18). We failed to find any relation between the shape of spectrum and plant species or the

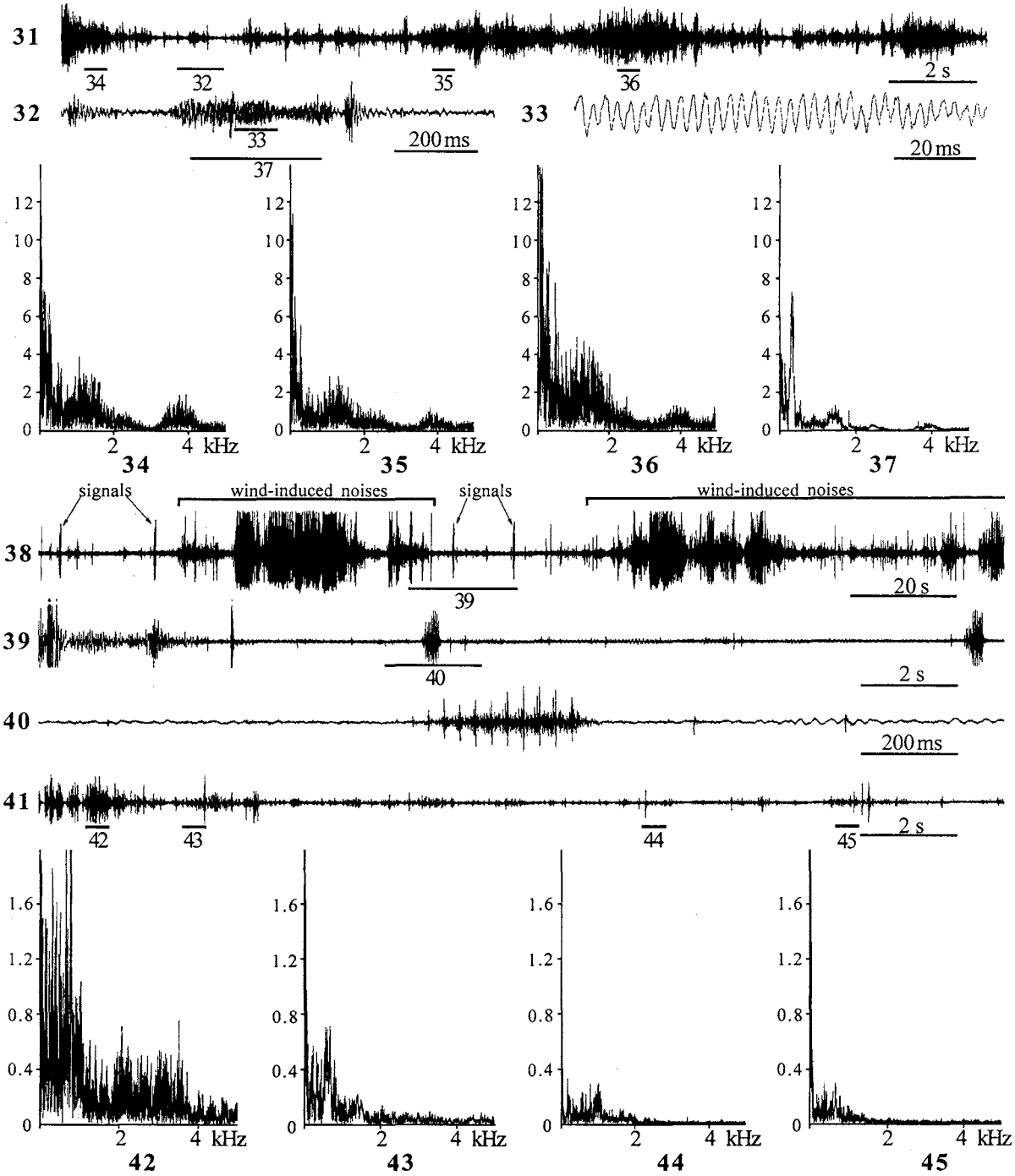


Figs 19–30. 19–24 — *Gargara genistae* on *Cytisus ruthenicus* (No.1 in the Table): 19 — oscillogram of wind-induced vibrations and calling signal; 20 — same, calling signal; 21–22 — spectrograms of wind-induced vibrations; 23–24 — same, different parts of calling signal; 25–30 — *Craspedolepta nervosa* on *Achillea millefolium* (No.9 in the Table): 25 — oscillogram of wind-induced vibrations and calling signal, 26 — same, calling signal, 27–29 — spectrograms of wind-induced vibrations, 30 — same, calling signal. Parts of signals indicated as 20–24 and 26–30 are given on oscillograms and spectrograms under the same numbers. Y-axis of spectrograms is graduated in per-unit notation.

Рис. 19–30. 19–24 — *Gargara genistae* на *Cytisus ruthenicus* (№ 1 в таблице): 19 — осциллограмма вызванных ветром колебаний и призывного сигнала; 20 — то же, призывный сигнал; 21–22 — спектрограммы вызванных ветром колебаний; 23–24 — то же, разные фрагменты призывного сигнала; 25–30 — *Craspedolepta nervosa* на *Achillea millefolium* (№ 9 в таблице): 25 — осциллограмма вызванных ветром колебаний и призывного сигнала; 26 — то же, призывный сигнал; 27–29 — спектрограммы вызванных ветром колебаний; 30 — то же, призывный сигнал. Фрагменты сигналов, обозначенные цифрами 20–24 и 26–30, представлены на осциллограммах и спектрограммах под такими же номерами. Масштаб по оси Y на спектрограммах — в условных единицах.

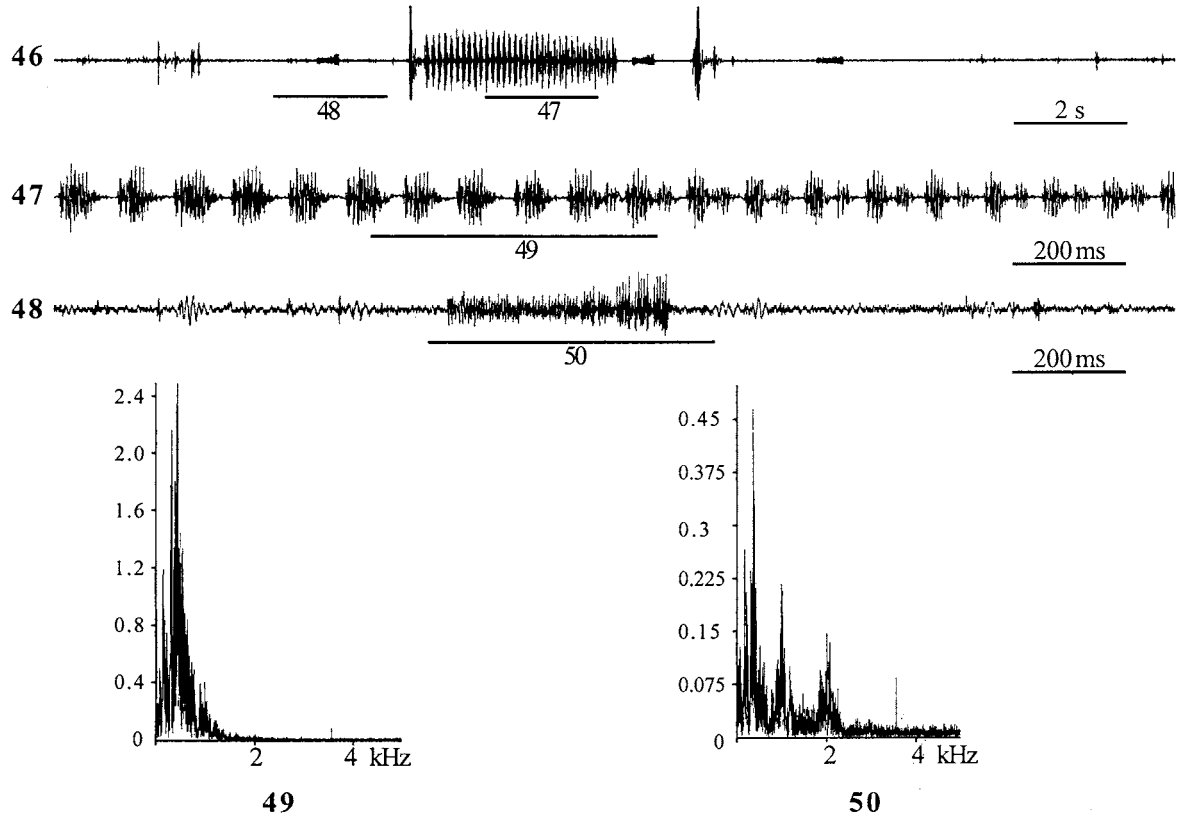
height and other properties of the stem basing on our material. Similar data were obtained by Cocroft and Rodríguez [2005] for two species of trees. Apparently, this pattern is intrinsic to the most part of vibratory noises induced in plants irrespective of their species, shape and other characteristics.

In most cases, the main part of spectra of vibratory signals of Psyllinea and small Auchenorrhyncha occupy the range above 1 kHz. For this reason, sometimes it is believed that insects using vibratory signals have separate communication cannel free of noises at their disposal. This seems to be the case if the wind is mod-



Figs 31–45. 31–37 — *Aglena ornata* on *Bolboschoenus maritimus* (No.2 in the Table): 31 — oscillogram of wind-induced vibrations and calling signal; 32 — same, calling signal; 33 — same at a higher speed, showing the shape of vibrations in a signal; 34–36 — spectrograms of wind-induced vibrations; 37 — same, calling signal; 38–40 — oscillograms of calling signals of *Criomorphus albomarginatus* and wind-induced vibrations in the stem of *Calamagrostis epigeios* (No.7 in the Table); 41–45 — vibrations induced in the stem of *C. epigeios* by the beetle, *Dermestes* sp. (Dermestidae) moving along the surface of the soil at the distance from 2 up to 7–8 cm from the base of the stem (No.7 in the Table): 41 — oscillogram, 42–45 — spectrograms of different parts of the recording. Parts of signals indicated as 32–37, 39–40 and 42–45 are given on oscillograms and spectrograms under the same numbers. Y-axis of spectrograms is graduated in per-unit notation.

Рис. 31–45. 31–37 — *Aglena ornata* на *Bolboschoenus maritimus* (№ 2 в таблице): 31 — осциллограмма вызванных ветром колебаний и призывного сигнала; 32 — то же, призывный сигнал; 33 — то же на более высокой скорости развертки, показана форма колебаний в сигнале; 34–36 — спектрограммы вызванных ветром колебаний; 37 — то же, призывный сигнал; 38–40 — осциллограммы призывных сигналов *Criomorphus albomarginatus* и вызванных ветром колебаний в стебле *Calamagrostis epigeios* (№ 7 в таблице); 41–45 — колебания, вызванные в стебле *C. epigeios* жуком *Dermestes* sp. (Dermestidae), движущимся по поверхности почвы на расстоянии от 2 до 7–8 см от основания стебля (№ 7 в таблице): 41 — осциллограмма; 42–45 — спектрограммы разных частей записи. Фрагменты сигналов, обозначенные цифрами 32–37, 39–40 и 42–45 представлены на осциллограммах и спектрограммах под такими же номерами. Масштаб по оси Y на спектрограммах — в условных единицах.



Figs 46–50. *Graphocraerus ventralis* and *Craspedolepta nervosa* on *Achillea millefolium* (No.10 in the Table): 46 — oscillogram of calling signals of two species; 47 — same, *G. ventralis*; 48 — same, *C. nervosa*; 49 — spectrogram of calling signal of *G. ventralis*; 50 — same, *C. nervosa*. Parts of signals indicated as 47–50 are given on oscillograms and spectrograms under the same numbers. Y-axis of spectrograms is graduated in per-unit notation.

Рис. 46–50. *Graphocraerus ventralis* и *Craspedolepta nervosa* на *Achillea millefolium* (№ 10 в таблице): 46 — осциллограмма призывных сигналов двух видов; 47 — то же, *G. ventralis*; 48 — то же, *C. nervosa*; 49 — спектрограмма призывного сигнала *G. ventralis*; 50 — то же, *C. nervosa*. Фрагменты сигналов, обозначенные цифрами 47–50, представлены на осциллограммах и спектрограммах под такими же номерами. Масштаб по оси Y на спектрограммах — в условных единицах.

erate and the amplitude of a signal is comparable with this of background noises. Under such conditions communication signal as a rule can be distinguished against wind-induced vibrations with more or less success (Figs 19–37). Still, if the amplitude of plant movements is high, especially in thickets, where stems and leaves touch each other, the amplitude of noises far exceeds this of the signal. In such situation high-frequency components of noises can jam a signal and communication became impossible.

There are several possible ways for insects to avoid wind-induced noises. The first way is to sing during short periods of lull, i.e. to insert signals into pauses between noises. Our observations on *Criomorphus albomarginatus* (Curtis, 1833) (recordings Nos.7–8 in the Table) show that at least in certain cases insects actually use this possibility. During half-an-hour period of recording males have never produced signals during the wind rushes, but chose for singing rather prolonged periods of silence (about 30 s and more) (Figs 38–40).

As it was noted above, average wind velocity measured by anemometer does not adequately depict actual situation in any individual point. Even a local hollow with a depth about 10 cm can provide sufficient shelter in a windy day. Recordings Nos.9–10 (Table) were made under such conditions in the open place in the valley of Moskva River, but due to the fact that the plant was growing in a small hollow, the influence of wind was minimal. Amplitude of movements of the tip of the stem has not exceeded 0.5 cm; in addition, no other stems touched the plant to which the recording equipment was connected. As a result, the recordings made in nature had almost the same quality, as these obtained under laboratory conditions (Figs 46–48). Therefore, the second possible way to avoid wind-induced noises is choosing the most sheltered places and/or rather sparse vegetation for singing.

Furthermore, it is well known that in steppes and deserts, where the effect of wind on vibratory communication is most strong, the change of wind intensity during a day follows certain pattern. Typically, wind velocity reaches its maximum in the middle of a day, whereas in the morning and in the evening wind almost ceased. We have no information on changes of acoustic activity of small Homoptera during a day. It is possi-

ble, however, that in steppes and deserts forms producing vibratory signals can avoid the period of high wind velocity by shifting the peaks of singing activity to the morning and evening hours.

Mechanical activity of other insects appeared to be far less important source of background noises in the region of our investigations. As a rule, insects are not numerous enough to produce constant and high-amplitude noises making vibratory communication impossible. Nevertheless, sometimes these noises exceed communication signals in amplitude. Their frequency spectra do not differ principally from these of wind-induced vibrations (Figs 41–45). Consequently, in the places, where the density of permanently moving insects is high (e.g. near the ant nests), vibratory noises resulting from their activity can interfere with signals of Homoptera.

Spectra of vibratory signals of different species occupy approximately the same frequency range with upper limit not exceeding 4–5 kHz (Figs 49–50). Thus, several individuals singing simultaneously are the source of noises for each other. If the songs have different amplitude (Figs 46–48), low-amplitude signal can be absolutely indistinguishable against the high-amplitude one. Still, this seems to be rather rare case, because, as it was mentioned above, the density of insects on the plant usually is not high. Moreover, vibratory signals of small Homoptera for the most part are short phrases having duration up to 20–30 s. In contrast with singing cicadas, katydids and crickets, small Cicadinea and Psyllinea as a rule does not produce their songs ceaselessly, but sing with rather long irregular intervals. The probability of overlapping of such signals is much lower than for continuous songs, which helps to avoid competition for acoustic transmission channels.

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