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Vibrational Background Noise in Herbaceous Plants and Its Impact on Acoustic Communication of Small Auchenorrhyncha and Psyllinea (Homoptera)

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Abstract—Vibrations induced in plant stems by rain drops, wind, and mechanical activity of insects were studied under natural conditions. Wind and rain can induce high-frequency vibrations in the range up to 3–4 kHz and jamming insect signals completely. For this reason, small homopterans mostly emit their signals during the gaps between gusts of wind. In the regions where strong wind blows during most part of the day, they concentrate mainly in the places protected from the wind (dry river beds, hollows, and other depressions of the relief). Individuals of different species occurring on the same or neighboring plants usually sing alternately, i.e., demonstrate the same response to each other's signals as to the wind-induced noise. Low-amplitude vibrations resulting from insect movements have no considerable impact on vibrational communication of Homoptera.

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The main task of insect bioacoustics has always consisted in studying the acoustic signals per se and describing them by oscillograms, sonograms, and other methods. Correspondingly, researchers have always tried to obtain high-quality, "clear" records without any unrelated noise, or to filter this noise out during signal processing. The fact that under natural conditions, insects themselves face the problem of isolating the valid signal from various kinds of noise, has been largely neglected. The possible role of noise as a factor shaping the physical parameters of the signal (Polajnar and Čokl, 2008) has also been generally overlooked.

In addition, bioacoustics has for a long time been dealing only with insects that emit sounds in the narrow sense, i.e., air-borne waves: these are mostly orthopterans and the singing cicadas (Homoptera, Cicadidae). Only in the two recent decades it has become evident that these groups represent an exception rather than the rule, whereas most species from other insect taxa use vibrational communication signals transmitted through solid substrates (Cocroft and Rodríguez, 2005).

Even now, insect vibroacoustics is almost completely confined to laboratories, because low-amplitude vibrational signals are usually recorded with bulky equipment that is unsuitable for field studies. For this reason, there are only several publications devoted to the study of vibrational noise. The range of potential natural sources of this kind of noise is comparatively small: it includes the wind, atmospheric precipitation, mechanical and acoustic activity of animals, and in some cases, loud sounds capable of inducing vibrations in solid bodies (Saxena and Kumar, 1980; Cocroft and Rodríguez, 2005). It is obvious that imitation of such noise in the laboratory (for example, imitation of wind noise with a blower, or imitation of rain noise with drops of liquid from a pipette) cannot reproduce the natural situation in its entirety and may result in a distorted assessment of the physical parameters of noise and their effects on the insect communication.

The noise induced by biotic and abiotic factors in the leaves of banana and agave was studied within the framework of a comprehensive research of vibrational communication in spiders of the genus *Cupiennius* (Araneae, Ctenidae) (Barth et al., 1988). The wind-induced vibrations were found to have very low frequencies: the main peaks in their frequency spectrum were positioned at about 10 Hz while the upper boundary of the spectrum reached 50 Hz. Frequencies as high as 200 Hz could be detected in this noise only after considerable amplification. Drops of rain induced vibrations with higher frequencies, up to approximately 250 Hz. Vibrations caused by mechanical activity of insects (in the cited work, by a cockroach moving over the leaf) were characterized by wide-band noise spectra with the upper boundaries at about 900 Hz and maxima within the range of 400–700 Hz. At the same time, some insects representing the potential prey could move almost noiselessly and did not induce the characteristic “prey alert” response in spiders.

Analysis of vibrations induced at a wind velocity of 1–2 m/s in the shoots of two arboreal plant species also showed that the noise energy was mostly concentrated within the range of 20–30 Hz and decreased abruptly at higher frequencies (Cocroft and Rodríguez, 2005). However, the cited authors emphasized that even within the range of 100–1000 Hz used for vibrational communication by most insects, the noise amplitude might be great enough to jam their signals.

My later studies (Tishechkin, 2007a) showed that under the conditions of European Russia, the noise induced by wind in plant stems always included high-frequency components with significant amplitudes, for example, additional peaks within the range of 2–4 kHz. Thus, the frequency ranges of the noise and the signals of small insects were found to overlap completely. Such differences in the results may be due to the fact that the preceding researchers mostly recorded oscillations in isolated leaves or shoots; however, in the dense grass stand all the stems are in contact, and high-frequency vibrations in them may be produced not by the wind itself but by the friction and collision of various parts of the plants. Oscillations produced by mechanical activity of insects occupy almost the same frequency range.

Wind is one of the principal sources of vibrational noise in the nature; therefore, males of Homoptera mostly emit their signals during the short gaps between gusts of wind (Tishechkin, 2007a; McNett et al., 2010). By the example of an American treehopper species (Auchenorrhyncha, Membracidae) it was shown that females less readily responded to male signals as the signal-to-noise ratio decreased. In addition, in territories where the wind intensity changed regularly depending on the time of day, the maximum acoustic activity of these insects coincided with the calm period (McNett et al., 2010).

Unfortunately, the above studies were mostly carried out on a few model arthropod and plant species, some of them under the laboratory conditions (McNett et al., 2010). In order to determine whether their results reflect some general trends or merely special cases, one should study other species under natural conditions and in different landscapes. This communication reports the results of my field study of vibrational noise in the herbaceous plant communities in the central part of European Russia.

MATERIALS AND METHODS

The low-amplitude vibrational signals in plant stems were recorded using a GZP-311 piezoelectric cartridge (a pickup head of a vinyl record player) connected to a Sony Walkman MZ-NH900 recorder via a matching amplifier similar in design to the preamplifiers used in phonographs with piezoelectric pickups. To avoid amplitude distortions the option of manual recording level adjustment was used.

Data on the plant and insect species, localities, and the conditions of signal recording are summarized in table. All the records in Moscow Province were made by myself in the nature; the signals of *Symphypyga repetekia* Kusn. (Auchenorrhyncha, Cicadellidae) in Astrakhan Province were recorded by N.A. Burlak in the laboratory. For the field recordings, the cartridge was positioned on the ground with its stylus touching the plant, so as to minimize the extra mass added to the stem. Since in the dense grass stand each plant touches its neighbors in many points, the contact with the cartridge did not modify the natural situation.

The insects were collected in the same biotope immediately before recording and released onto the plant to which the cartridge was attached. Some individuals flew away but others remained on the experimental stem or on neighboring stems and started emitting vibrational signals shortly after. Besides, signals of other species inhabiting the same biotope which happened to be nearby were also sometimes recorded.

The records were analyzed on a PC equipped with an L-305 analog/digital converter (L-Card Ltd, Moscow) and the corresponding software.

The recording equipment was not calibrated; therefore, no scale is indicated for the amplitude axis in the frequency spectra (the vertical axis in Fig. 1, *4–6* and the horizontal axis in Fig. 3, *1*, inserts *a* and *b*).

RESULTS AND DISCUSSION

Noise Produced by Atmospheric Precipitation

The vibrations induced in an apple-tree leaf by a small metal ball or a drop of liquid falling on it were

Localities, plant and insect species studied, and the conditions of signal recording

No.	Locality	Plant species and the recording conditions	Insect species and temperature during recording
1	Moscow Prov., Voskresensk Distr., env. of Beloozerskii	*Ribes rubrum* L. (Grossulariaceae), *Mentha* sp. (Lamiaceae), *Plantago major* L. (Plantaginaceae); dead calm weather, weak rain	–
2	Ca. 60 km N of Astrakhan, env. of Dosang, barchan sands	*Calligonum aphyllum* Guerke (Polygonaceae), in laboratory	*Symphypyga repetekia* Kusn. (Auchenorrhyncha, Cicadellidae), 33–35°C
3	Moscow Prov., Serpukhov Distr., the Oka floodlands near Luzhki	*Artemisia vulgaris* L. (Asteraceae), plant 18 cm tall among low grasses contacting it with their blades; in the wind, plant tip swings with amplitude of up to 5 mm; ants moving on the ground create continuous background noise	*Bactericera calcarata* Schaef. (Psyllinea, Triozidae), 33°C
4	Moscow Prov., Voskresensk Distr., env. of Beloozerskii	*Anethum graveolens* L. (Apiaceae), isolated plant 80 cm tall; in the wind, plant tip swings with amplitude of up to 4–5 cm	Larva of *Papilio machaon* L. (Lepidoptera, Papilionidae), sitting 65 cm from the ground; male of *Aphrophora alni* (Fall.) (Auchenorrhyncha, Aphrophoridae) sitting on the same stem 30 cm from the ground, 27–28°C
5	Moscow Prov., Serpukhov Distr., the Oka floodlands near Pushchino-na-Oke	Unidentified grass (Poaceae), dense patch 20–25 cm tall, with multiple points of contact between plants; in the wind, tips of stems and blades swing with amplitude of 1.5–2.0 cm	*Graphocraerus ventralis* (Fall.) (Auchenorrhyncha, Cicadellidae), 22–25°C
6	Moscow Prov., Voskresensk Distr., env. of Beloozerskii	*Poa annua* L. (Poaceae) and *Trifolium repens* L. (Fabaceae), mixed dense patch about 10 cm tall, with multiple points of contact between plants; in the wind, tips of stems and leaves swing with amplitude of 0.5–1.0 cm	*Eupelix cuspidata* (F.) and *Doratura stylata* (Boh.) (Auchenorrhyncha, Cicadellidae), 35°C
7	Moscow Prov., Serpukhov Distr., the Oka floodlands near Luzhki	*Artemisia abrotanum* L. (Asteraceae), isolated plant 27 cm tall, not touching other stems; in the wind, tips of shoots and leaves swing with amplitude of 0.5–1.0 cm	*Craspedolepta alevtinae* Andr. (Psyllinea, Aphalaridae), 34–36°C
8	Moscow Prov., Voskresensk Distr., env. of Beloozerskii, the Moskva floodlands	*Achillea millefolium* L. (Asteraceae), stem 42 cm tall among low grasses (on average about 15 cm tall), with multiple points of contact between plants; in the wind, tip of stem swings with amplitude of 0.5–1.0 cm	*Craspedolepta nervosa* (Först.) (Psyllinea, Aphalaridae) and unidentified species of Delphacidae (Auchenorrhyncha), 30°C

studied in the laboratory by a group of European authors (Casas et al., 1998). The resulting vibrational burst was found to have a typical impact signature with a steep leading edge, a sloping trailing edge, and frequency decreasing from the beginning to the end of the oscillation process. No essential differences were found between the vibrations caused by the fall of a water drop or a solid object and those caused by the landing of a small insect (a species of Eulophidae, Hymenoptera).

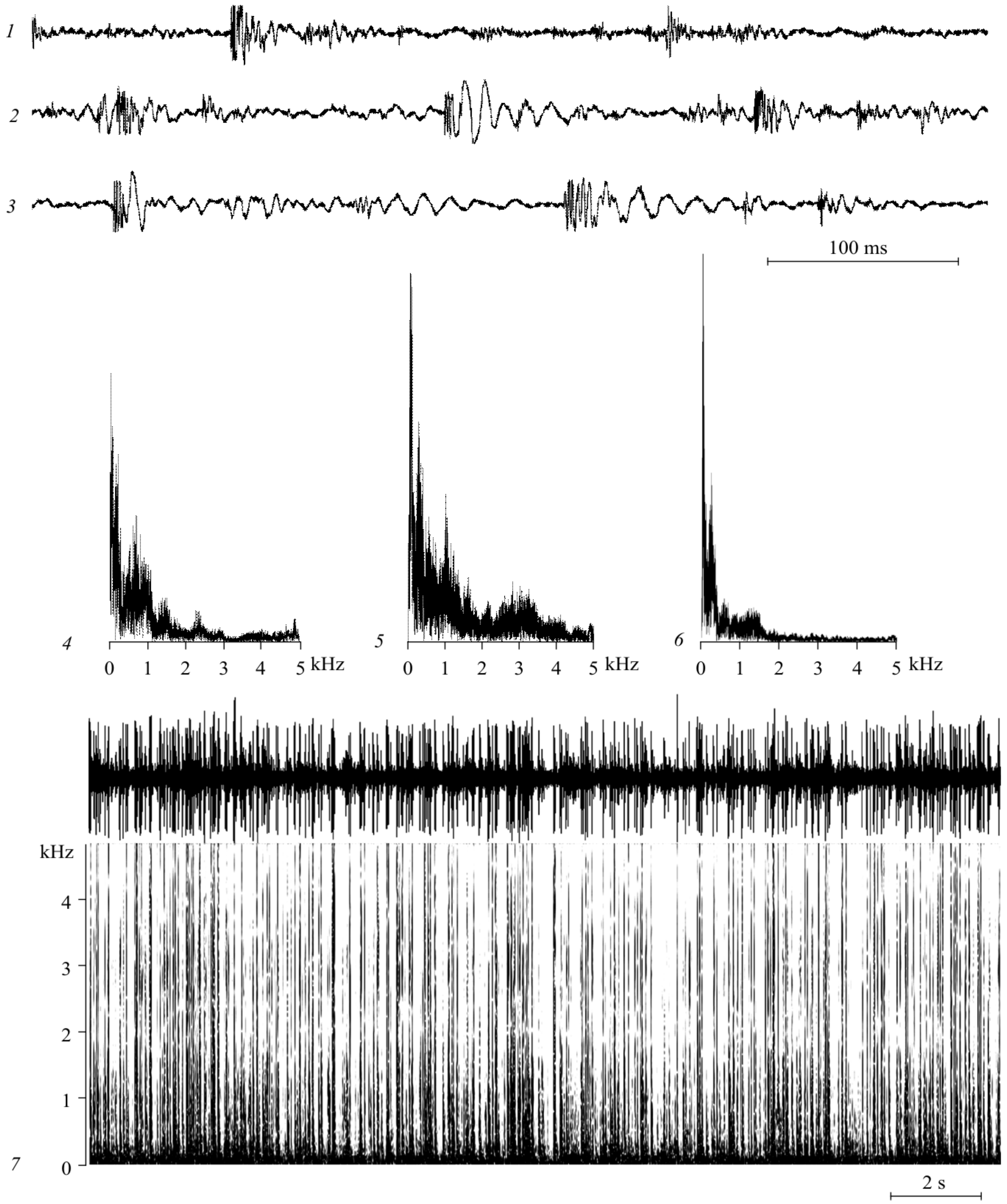

Fig. 1. Vibrations induced in plant stems and leaves by falling rain drops. *1–3*, oscillograms (*1*, *Ribes rubrum*; *2*, *Plantago major*; *3*, *Mentha* sp.); *4–6*, frequency spectra based on analysis of 0.5-s record samples, with a linear scale on the vertical axis (*4*, *Ribes rubrum*; *5*, *Plantago major*; *6*, *Mentha* sp.); *7*, oscillogram and sonogram at the same scale, *Plantago major*.

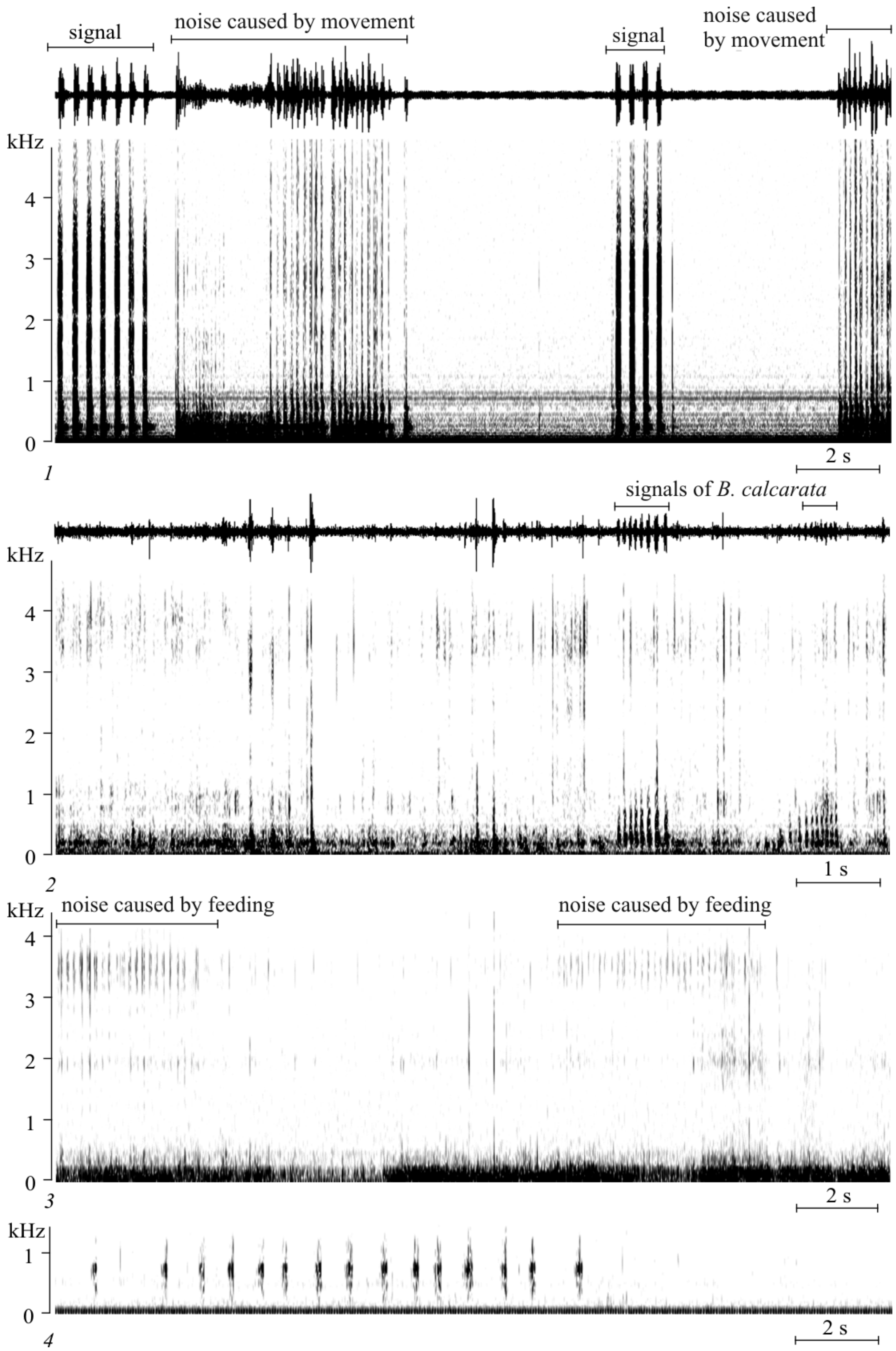

Fig. 2. Vibrational noise induced in plant stems by mechanical activity of insects, and the calling signals of Homoptera: *1*, *Symphypyga repetekia*, signals of a male alternating with noise produced by the same male moving over the stem; *2*, *Bactericera calcarata*, signals of males against the background noise produced by ants moving on the ground near the plant; *3*, noise produced by a feeding larva of *Papilio machaon*; *4*, a calling signal of *Aphrophora alni*. *1*, *2*, oscillogram and sonogram at the same scale; *3*, *4*, sonogram.

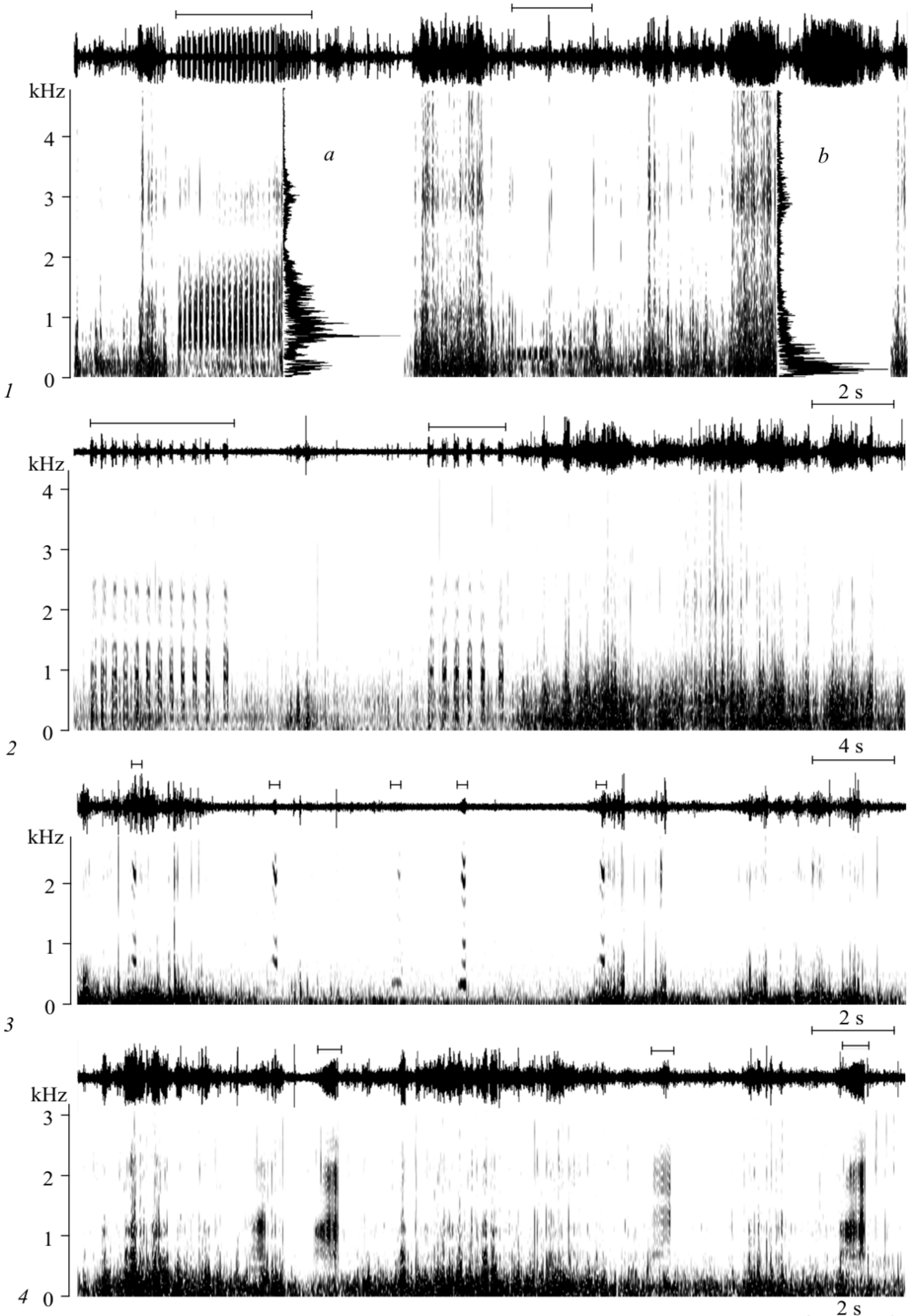

Fig. 3. Vibrational signals of Homoptera against the background noise induced in plant stems by the wind: *1*, calling signals of *Graphocraerus ventralis* and noise at a moderate wind velocity, oscillogram and sonogram at the same scale; inserts *a* and *b* in the sonogram represent frequency spectra of 0.5-s record samples immediately preceding the inserts, with a linear scale on the horizontal axis; *2*, calling signals of *Eupelix cuspidata* and noise at a moderate wind velocity, oscillogram and sonogram at the same scale; *3*, the same for *Craspedolepta alevtinae*; *4*, the same for *C. nervosa*. The calling signals are designated by horizontal bars above the oscillograms.

We have recorded vibrations induced in the stems of the red currant *Ribes rubrum* L. (Grossulariaceae) and the mint *Mentha* sp. (Lamiaceae) and in the leaf stalk of the greater plantain *Plantago major* L. (Plantaginaceae), by moderate rain under the natural conditions (table, No. 1). The vibrations induced by individual drops of water were generally similar to those recorded in the laboratory, even though their shapes were more diverse than under the standardized conditions of a laboratory experiment (Fig. 1, *1–3*). The frequency spectra of vibrations in the currant and plantain stems extended to at least 4–5 kHz (Fig. 1, *4*, *5*), and those in the mint stem, approximately to 2 kHz (Fig. 1, *6*). The high-frequency component of vibrations is known to attenuate faster in substrates with a lower elastic coefficient (Michelsen et al., 1982). It may be assumed that the observed differences were related to the different elasticity of the studied plant stems: the high-frequency vibrations attenuated faster in the relatively "soft" mint stem that in the more rigid plantain leaves and currant stems.

It has been shown previously that even though the vibrational signals of small homopterans (Auchenorrhyncha, Cicadellidae and Delphacidae) yield in amplitude to the signals produced by falling water droplets, they can still be transmitted from one plant to another through contacts of their overground and underground parts (Tishechkin, 2011). Therefore, during the rain, the cartridge installed at any point of the stem can record vibrations induced by droplets hitting all the other parts of this stem and the neighboring plants touching it. As a result, the hits of individual droplets merge into uniform continuous noise, against the background of which the valid vibrational signals will most probably be indiscernible (Fig. 1, *7*). During summer in the temperate zone, precipitation is usually accompanied by a decrease in temperature and, correspondingly, the activity of insects; under such conditions, the role of the rain as a source of acoustic interference may be not very significant. However, in the tropical forest zone the rain may significantly influence the vibrational communication of small insects.

Noise Produced by the Mechanical Activity of Insects

It is known that during recording of vibrational signals of leafhoppers or psyllids, the noise accompanying their mechanical activities, such as movement, cleaning of integuments, etc., is also quite discernible. For example, if the singing insect is moving over the plant, the induced vibrations may be comparable to the communication signals and occupy the same frequency range. The recorded calling signals of a male of *Symphypyga repetekia* Kusn. (Auchenorrhyncha, Cicadellidae) and the noise produced by its movement are given as an example (Fig. 2, *1*; No. 2 in table). Given the high abundance of insects under the natural conditions, for example, near ant nests, such noise may be nearly continuous.

Our studies in the nature have shown that the vibrational signals emitted by an insect sitting on a plant cannot be jammed by the noise produced by other insects moving on the ground near the plant or on the neighboring stems. For example, during recording signals of *Bactericera calcarata* Schaef. (Psyllinea, Triozidae) on a wormwood stem, the noise produced by ants moving nearby formed an almost constant background. The upper boundary of its frequency range reached 4.5 kHz; the lower boundary could not be determined because the frequency range below 500 Hz was filled with the wind noise (Fig. 2, *2*; No. 3 in table). However, the recorded psyllid signals could be easily distinguished in the earphones and were clearly discernible in the sonogram. This result was quite natural since the ants were similar in size to small homopterans, so that noise produced by them could not much surpass the communication signals.

The larvae of many lepidopterans have a considerably greater body mass than leafhoppers or psyllids. It might therefore be expected that vibrations caused by the mechanical activity of such larvae would have sufficiently high amplitudes to completely jam the signals of Homoptera. However, this assumption was not confirmed by experiments under natural conditions.

We studied the noise that accompanied feeding and movement of the last-instar larvae of the swallowtail *Papilio machaon* L. (Lepidoptera, Papilionidae), about 3.5 cm long, positioned on the dill *Anethum graveolens* L. (Apiaceae) (No. 4 in table). The short amplitude bursts produced by rhythmic movements of their mouthparts during feeding occupied the approximate frequency range between 2 and 4 kHz and were usually not very distinct in the sonograms (Fig. 2, *3*). The noise produced by a larva moving over the plant could not be recorded due to insufficient sensitivity of our equipment. The signals of the spittlebug *Aphrophora alni* (Fall.) (Auchenorrhyncha, Aphrophoridae), only 0.8 cm long, which happened to be present on the same stem, had a noticeably higher

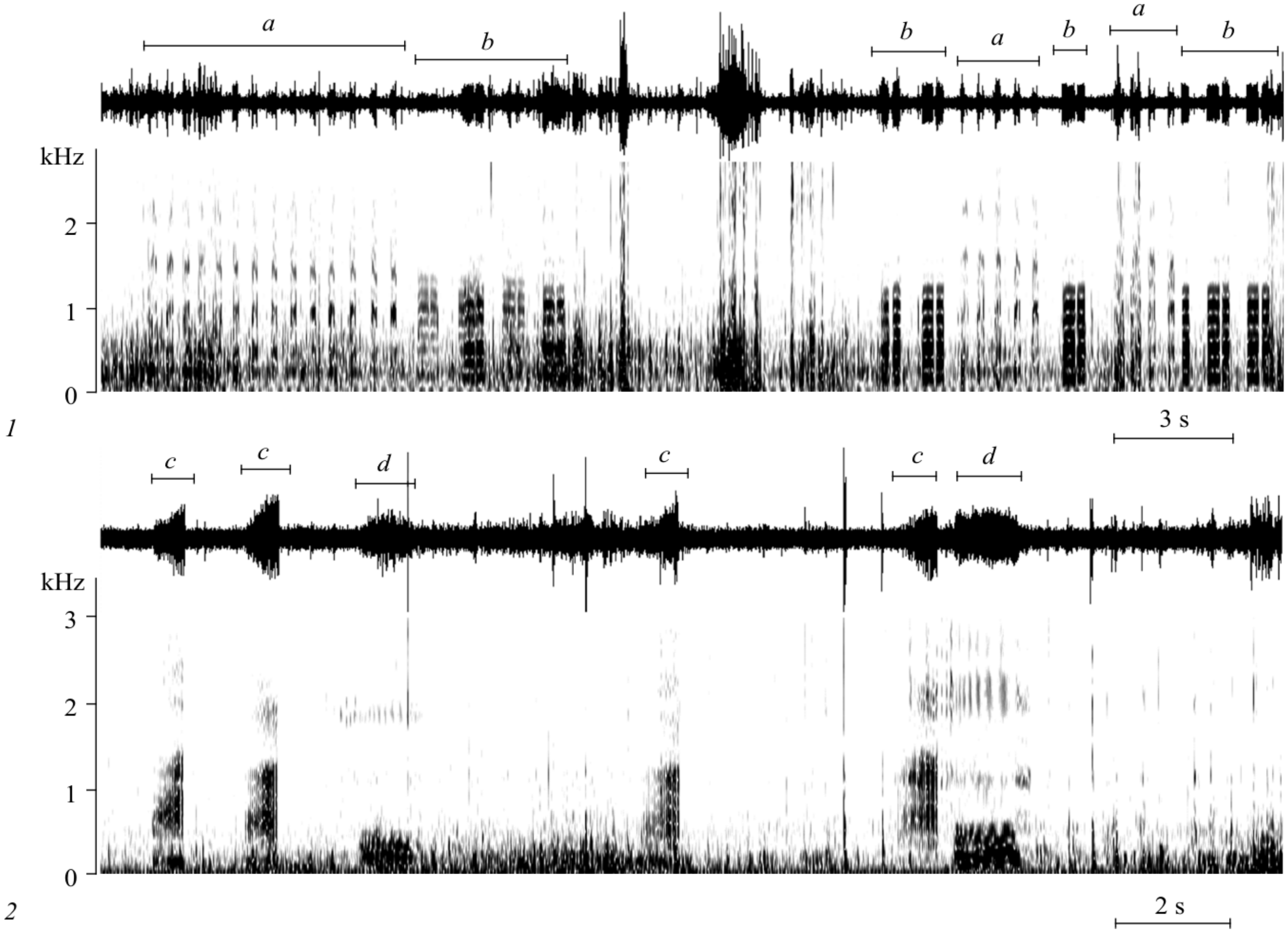

Fig. 4. Vibrational signals of different species of Homoptera singing by turns close to one another; the signals are designated by horizontal bars with letters above the oscillograms: *1*, *Eupelix cuspidata* (*a*) and *Doratura stylata* (*b*), oscillogram and sonogram at the same scale; *2*, the same, *Craspedolepta nebulosa* (*c*) and an unidentified species of Delphacidae (*d*).

amplitude when recorded at the same amplification level (Fig. 2, *4*; No. 4 in table).

The frequency characteristics of plants are highly nonlinear, so that the signal propagating in the plant stems does not decrease uniformly with distance from its source (Michelsen et al., 1982). For this reason, the amplitudes of vibrations produced by different individuals cannot be compared under natural conditions, even with calibrated equipment. Still, considering the significant differences in the size and body mass of the insects studied, it may be assumed that lepidopteran larvae demonstrate a greater degree of “quietness” as compared to homopterans.

The fact that some phytophagous insects can move with almost no noise was pointed out by Barth and coauthors (1988). It is also known that parasitic hymenopterans find their hosts by vibrations caused by the mechanical activity of the latter, whereas the potential hosts, in their turn, stop feeding and moving when the parasitoid appears on the plant (Casas and Magal, 2006). The low level of noise accompanying the activity of lepidopteran larvae may render them less vulnerable to their natural enemies. Therefore, even though lepidopteran larvae are often present in great numbers on the plants and spend most of their time feeding, they can hardly produce sufficient vibrational noise to jam the communication of small homopterans.

The Effect of Wind-induced Noise on the Vibrational Communication of Homoptera

Vibrations induced by the wind in the plant stems and leaves occur in the frequency range with the upper boundary of at least 3–4 kHz, i.e., in the same range as the vibrational signals (Fig. 3, *1*; No. 5 in table). If the wind is strong, such noise can jam the insect signals completely. A question arises: how can homopterans use vibrational communication in open landscapes, for example, in the steppe or desert zones where dead calm weather is usually limited to the morning and evening hours?

Experiments with signals recorded in the nature have shown that the average wind velocity determined with an anemometer is almost unrelated to the level of noise recorded on a particular plant stem. First, as mentioned above, the most high-amplitude and high-frequency noise is produced by the friction and collision of plant parts, therefore the intensity of this kind of noise is much lower in sparse vegetation than in the dense grass stand. Second, any minor relief depression can provide some shelter from the wind, especially as far as herbaceous plants are concerned. Finally, under the conditions of European Russia, continuous high-amplitude noise was almost never recorded from a given plant stem for more than 10–15 min, even in a strong wind. Periods of noise always alternated with gaps during which the noise amplitude was only slightly greater than that under the laboratory conditions.

A similar pattern was observed in our experiments with three species of planthoppers: *Graphocraerus ventralis* (Fall.), *Eupelix cuspidata* (F.), and *Doratura stylata* (Boh.) (Auchenorrhyncha, Cicadellidae; Nos. 5, 6 in table) and two species of psyllids: *Craspedolepta alevtinae* Andr. and *C. nervosa* (Först.) (Psyllinea, Aphalaridae; Nos. 7, 8 in table). The noise produced by a sudden gust of wind would jam all the signals, making the communication impossible for several tens of seconds or even several minutes. The individuals which had been singing immediately before the gust, fell silent almost immediately. However, as soon as the calm interval began, they started emitting vibrational signals, "fitting" them between the periods of noise (Fig. 3). Signals more or less considerably overlapping with strong noise were never recorded in our material. Similar behavior was previously described for *Criomorphus albomarginatus* (Curtis, 1833) (Delphacidae; Tishechkin, 2007a) and in a species of Membracidae (McNett et al., 2010).

We have studied the signals with noise-like frequency spectra, which are characteristic of most homopterans. However, some leafhoppers have signals with line spectra which are represented by regular sine waves in high-speed oscillograms (Tishechkin, 2001, 2007a). In the opinion of Cocroft and Rodríguez (2005), prolonged pure-tone signals can be more easily distinguished against the continuous noise background and may thus represent an advantage in a particularly noisy environment. Although this reasoning appears to be true, it should be noted that species emitting pure-tone signals, for example, representatives of Typhlocybinae and Paralimnini (Auchenorrhyncha, Cicadellidae; Tishechkin, 2001, 2007b), can be found under a great variety of habitats, coexisting with the forms that emit wide-band noise signals.

Another possible way for small insects to avoid noise may be living in places protected from the wind (Tishechkin, 2007a). This assumption was confirmed by our observations in the Barguzin Depression (Buryatia), where strong winds blow almost constantly due to the air pressure differential between the Lake Baikal area and the surrounding mountain ranges. In the steppified part of the depression, planthoppers were found only in the depressed relief forms: hollows, dry river beds, etc. These insects were present in negligible numbers (no more than 1–2 ind. per 60 standard net-sweeps) or completely absent in the plain steppe and floodland meadow patches, in spite of the well-developed, practically undisturbed vegetation.

Thus, in areas affected by winds during most of the day, vibrational communication becomes virtually impossible in the open biotopes; this factor may affect the abundance of insects and their distribution over the landscape.

The Response of Homoptera to Vibrational Signals of Sympatric Species

When studying signals of a particular species under natural conditions, we often recorded signals of other insects which happened to be near the plant from which recording was being made. Besides, in some experiments we intentionally released individuals of two different species onto the same plant in order to study their response to one another's signals. Since low-amplitude vibrations can be quite easily transmitted from plant to plant during physical contact (Tishechkin, 2011), the signals of several species being discernible in the same place should be a fairly common situation in the nature.

We have studied the acoustic interaction between individuals of *Eupelix cuspidata* and *Doratura stylata* situated on the same group of plants (No. 6 in table); in the process, we also managed to record the signals of a male *Lepyronia coleoptrata* (L.) (Auchenorrhyncha, Aphrophoridae) singing nearby. Besides, when recording the signals of *Craspedolepta nervosa* in the nature, we repeatedly recorded the signals of various planthoppers situated on the same or neighboring plant stems (No. 8 in table). Not all of these individuals were captured, therefore in some cases the planthoppers could not be identified to species. In the above situation, insects of different species always emitted their signals by turns, with no essential overlap of the signals being observed (Fig. 4).

It is known that many animals using acoustic communication tend to avoid interference of their own signals and those of their neighbors (see, e.g., Ficken et al., 1974). When this phenomenon occurs in groups of conspecific individuals, it is usually regarded as an example of cooperation (Greenfield, 1994). However, the response of homopterans to heterospecific signals does not differ in any way from their response to the wind noise: each individual times its signals to intervals between the signals of the other species. Thus, planthoppers and psyllids treat the signals of sympatric forms as noise, in the same way as they treat the vibrations caused by abiotic factors.

It is known that, despite the different signal structure, mutual acoustic interference of different species may be so great as to cause their segregation in terms of daily activity or seasonal development patterns (Wolda, 1993; Tishechkin, 2010). A case of vicariance, probably related to competition for the vibrational communication channels, was recently described for two close species of *Macropsis* (Auchenorrhyncha, Cicadellidae) living on *Berberis* spp. (Berberidaceae) (Tishechkin, 2012). It may therefore be concluded that the signals of sympatric species may represent one of the main sources of acoustic interference for small homopterans, apart from the noise caused by the wind and precipitation.

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