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Acoustic Irradiation Produced by Flying Moths (Lepidoptera, Noctuidae)

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Abstract—Characteristics of acoustic waves accompanying the flight of noctuid moths (Noctuidae) were measured. The low-frequency part of the spectrum is formed of a series of up to 17 harmonics of the wingbeat frequency (30-50 Hz) with a general tendency toward the decrease in the spectral density and the increase in the sound frequency. The root-mean-square level of the sound pressure from flapping wings was found to be 70-78 dB SPL. Besides low-frequency components, the flight of moths was accompanied by short ultrasonic pulses, which appeared with every wingbeat. Most of the spectral energy was concentrated within a range of 7-150 kHz with the main peaks at 60-110 kHz. The short-term pulses were divided into two or more subpulses with different spectra. The high-frequency pulses were produced at two phases of the wingbeat cycle: during the pronation of the wings at the highest point and at the beginning of their upward movement from the lowest point. In most of the specimens tested, the peak amplitude of sounds varied from 55 to 65 dB SPL at a distance of 6 cm from the insect body. However, in nine noctuid species, no high-frequency acoustic components were recorded. In these experiments, the acoustic flow from the flying moth within a frequency range of 2 to 20 kHz did not exceed the self-noise level of the microphone amplifier (RMS 18 dB SPL). Probable mechanisms of the high frequency acoustic emission during flight, the effect of these sounds on the auditory sensitivity of moths, and the possibility of their self-revealing to insectivorous bats are discussed. In addition, spectral characteristics of the moth echolocation clicks were more precisely determined within the higher frequency range (>100 kHz).

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As known, many nocturnal lepidopterans, and noctuid moths (Noctuidae) in particular, are hunted by many bat species (Milyanovskii, 1970; Swift and Racey, 1983; Anderson and Racey, 1991; Funakoshi and Yamamoto, 1996; Rostovskaya et al., 2000). In the course of evolution, Noctuid moths developed a protective behavior based on the early auditory detection of predator's echolocation signals (Roeder and Treat, 1957, 1961; Roeder, 1964, 1966, 1969). As a response, many bat species decrease the amplitude of their own signals or stop them at all, basing mainly on the intensive location of sounds produced by a flying insect (Anderson and Racey, 1991; Faure et al., 1993; Faure and Barclay, 1994; Fullard and Dawson, 1997). Perception of sounds produced by flopping wings is also very important in situations when the potential victim is situated out of the zone of sensitivity of the predator echolocator (Airapetyants and Konstantinov, 1974). Thus, the decreasing of the noise accompanying the flight helps moths to minimize the risk of having been found by a predator.

The logic of studies of interrelations of bats and moths needs objective data on physical characteristics of acoustic flows, accompanying the flight of bats and moths both. The first published data concerned sounds produced by a moth pressed between fingers of the researcher (Anderson and Racey, 1993). To base the following investigations on these would be, however, unwise, because flight conditions in these experiments were far from the real ones. In the next year, another paper with the results of measuring of physical characteristics of ultrasonic noise-like flashes that appeared in moths synchronously with each wingbeat was published (Waters and Jones, 1994). The peak amplitude of these noises constituted ~60 dB SPL (Sound Pressure Level) at a distance of 1 cm from the moth; the spectrum was wide, with maximum of 60 kHz.

Flying moths make 30-50 wingbeats per second. During each stroke, their fore wings in the lowest position form an angle of 90-120° toward each other, whereas in the upper point they visibly touch each other. Rapid video recording demonstrated that that noise splashes were associated with the moment of contact of hind wings (Waters and Jones, 1994). On the basis of this fact, Waters and Jones (1994) assumed that clicks registered by them appeared in flying moths as a result of wing encounter.

The theme of flight noises became more relevant after obtaining of the data on the real acoustic sensitivity of intact moths. It appeared that values of thresholds of moth reactions expressed as the increase of click emission are very low, constituting 10-30 dB SPL (Vorontsov and Lapshin, 2002; Lapshin and Vorontsov, 2000, 2003, 2005a). Such high sensitivity expects that the level of self-produced noises accompanying the flight must be either the same or lower than the acoustic thresholds. At the same time, the amplitude of high-frequency impulses registered by Waters and Jones exceeded behavioral thresholds by two orders on average. Taking into account this contradiction, we decided to study the dynamics of generation and spectral parameters of sounds accompanying the flight and produced by moths during a "fixed" flight, i.e., in the same experimental conditions under which acoustic thresholds of these moths were measured earlier (Lapshin and Vorontsov, 2000; Vorontsov and Lapshin, 2002; Lapshin, 2005).

Within the frames of a problem of acoustic detecting of moths by predatory bats, both high- and low-frequency components of accompanying sounds can be important; low-frequency components possess the highest amplitude in the "short-range area". In this connection, we also give data on measuring of sounds produced by flying moths in the frequency diapason of 10 kHz and lower, but without subdivision of registered sounds into components of "long-range" and "short-range" area.

MATERIALS AND METHODS

The main volume of acoustic measurements was performed on moths *Amphipyra pyramidea* L. (37 specimens), *Blepharita satura* Schiff. (18 specimens), *Agrotis segetum* Schiff. (8), *Macdunnoughia confusa* Steph. (8), *Meganephria oxyacanthae* L. (6), *Scoliopteryx libatrix* L. (6), *Amphipyra perflua* F. (5), *Blepharita amica* Tr. (5), *Eupsilia satellitia* L. (4), *Autographa gamma* L. (4), and *Xestia c-nigrum* L. (4 specimens). Additionally, we also analyzed sounds produced during the flight by moths *Enargia paleacea* Esp., *Xestia baja* F., *Eurois occulta* L., *Tholera popularis* F., *Agrochola circellaris* Hufn., *A. macilenta* Hbn., *Hydraecia micacea* Esp. (2 specimens of each species); and *Catocala nupta* L., *Trachea atriplicis* L., *Diachrysia chrysitis* L., *Plusia festucae* L. (1 specimen of each species). A total of 122 moth specimens were used in our experiments. Moths were attracted by a KG220-1000-4 lamp (1 kW total power) or by attractants (fermenting beer-honey mixture).

Measurements were performed in laboratory (Kropotovo biological station of the Institute of Developmental Biology, Russian Academy of Sciences) in middle August-end of September 2004-2005.

Before the experiment, a moth was glued to a flexible lead that kept the flying insect in a limited space in front of a microphones situated at a distance of 5-6 cm above, below, to the left, and to the right of the flying insect. In each experiment, signals from one, two, or three microphones were recorded, in dependence of the stability of moth flight and goals of the experiment.

The first experiments demonstrated that the spectral level of sounds accompanying the flight at frequencies exceeding 5 kHz is usually lower than noises of measuring devices (the summarized spectrum of all kinds of noises at the microphone port); therefore, main measurements were made in different frequency diapasons with different microphones, in order to obtain the best ratio between the level of signals measured and noises of registration channels.

In this connection, apparently, it is necessary to explain relationships between noise and frequency characteristics of measuring microphones. The upper border of sensitivity of a wide-range condenser microphone is determined by the resonance of its membrane; the frequency of the resonance is the function of the membrane weight and the force of its longitudinal extension. In particular, by this reason high-frequency microphones possess a comparatively small diameter and correspondingly small weight of the membrane (the necessity to decrease the size of the membrane with the increase of the frequency diapason is also associated with the retaining of the given directional characteristics of the microphone). At the same time, microphones with smaller diameter are characterized by lower sensitivity, because the area of perception of the acoustic energy is proportional to the square membrane diameter. Thus, when the voltage at the microphone amplifier outlet is normalized, the use of a wide-range microphone needs stronger amplification. Correspondingly, the level of technical noises at the amplifier outlet will also be higher.

Taking into account noise limitations, the ability to measure low amplitude signals in our experiments could be better realized in the frequency diapason from 10 Hz to 20 kHz (MK 102 (RFT) microphone; diameter 1-inch; root-mean-square of equivalent input noise 18 dB SPL in frequency band 2-48 kHz). The use of a MK 201 (0.5-inch) microphone worsened noise characteristics of the measuring channel (root-mean-square of equivalent input noise 23 dB SPL), but widened the frequency band up to 35 kHz (taking into account corrections leveling amplitude-frequency characteristics of the measuring tract in the area of high frequencies). A B&K (Brüel & Kjær) 4135 (0.25-inch) microphone was used in the diapason up to 120 kHz. Root-mean-square level of self-produced input noise of this microphone constituted 43 dB SPL, taking into account the influence of a 2-120 kHz filter at the outlet of the microphone amplifier.

Measurements in the diapason of 2-160 kHz were performed with a complex of equipment produced by G.R.A.S. Company; it included 0.25-inch (40BF) or 0.125-inch exchangeable microphones, a 26AB preamplifier, and a 40HF power unit (when the 0.125-inch microphone was used, the level of the noise constituted 58 dB SPL). Records obtained with both types of microphones were later additionally corrected in the diapason of 100-160 kHz corresponding to calibration characteristics of the producer. Acoustic measurements in high frequency diapason were performed with microphones with removed protective caps.

In order to prevent overloading of amplifiers by intensive low-frequency signals produced during wing flops, the resulting frequency characteristic of the registration channel after first amplifying cascades was limited underneath by a first order filter (cut-off frequency 1 kHz). In experiments on registration of acoustic waves produced by a flying moth, a 1-inch MK 102 microphone together with a B&K 2203 amplifier in the regime of linear frequency characteristic was used as a receiver.

Amplitude-frequency characteristics of registration systems were controlled by a B&K 2235 measuring device supplied with a B&K 4135 microphone (0.25-inch). The control of congruence of the amplitude of output electric signals with real acoustic levels was also performed with a 05 000 MMF (VEB Metra Meβ Frequeztechnik) calibrator. Acoustic pressure of 20 μPa was selected as zero dB SPL (Sound Pressure Level).

After damping of high-frequency components of the noise (filter cut-off frequencies 20, 50, or 200 kHz, in dependence of the quantization frequency selected) and transformation of the impedance, signals from outlets of microphone amplifiers went to inlets of an L-783 (L-CARD) analogue-digital transformer (ADT). Measurements in frequency diapasons below 20 kHz were performed with a quantization frequency of 44.1 kHz; below 35 kHz, with 220.5 kHz; when 0.25-inch or 0.125-inch microphones, sensitive in diapasons up to 120 and 160 kHz, respectively, were used, the frequency of quantization was increased to 882 kHz.

For the "timing" of registered sounds with moth wing movements, impulses synchronized with wing-beats were recorded into a PC memory in parallel. For the formation of such synchronized impulses, a weak laser was placed laterally to the moth; this laser illuminated the fore wing surface when moving wing approached its uppermost point. Alternating light signal, reflected from wing surface, was registered by a photodiode sensor. After amplification and transformation into the rectangular form, the electric signal entered went to the ADT via a delay regulation device. In parallel, the same signal (as a synchronizer) could go to a light-diode stroboscope (duration of a separate flash 2 ms). With the use of such device, regulating the delay of a flash in relation to the synchronized impulse, correspondence between moments of generation of synchronized impulses and the stage of the wing-beat, to which the registered acoustic signals were timed, could be determined.

The duration of separate record fragments usually constituted 3-6 s (100-300 wingbeat periods of an experimental insect). Each registration was followed by recording of a control fragment; before this recording, the experimental moth was removed from the microphone sensitivity zone.

During providing of acoustic measurements we constantly kept in mind that any manipulations with an experimental moth could destroy wing integrity or structures adjoining wings (e.g., tegulae). As a result of such damages, formation of centers of mechanical instability on cuticular surface was quite possible. Deformation of these structures could be accompanied by clicks or other sounds untypical of the normal insect flight. In this connection, special attention was paid to cases of especially "quite" moth flight or to situations when clicks or other sounds appeared not in the beginning of the experiment but some time after the beginning of the experimental flight.

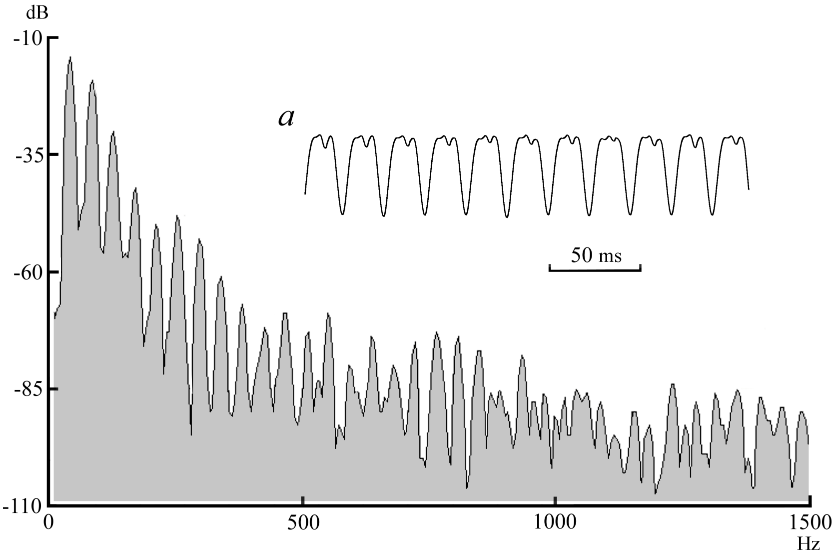

Fig. 1. Low frequency part of the spectrum of flight accompanying sounds in the moth *Agrochola circellaris.* Abscissas: frequency; ordinates: spectral density of auditory pressure. The level of 0 dB corresponds to spectral density of 0.05 Pa/Hz; (*a*) fragment of oscillograms of a signal from outlet of microphone amplifier (the microphone is situated above the flying insect).

Experiments were provided under the control of author's software. The data obtained were saved in a PC memory in a commonly accepted standard (Wave software, joint IBM and Microsoft product), that allows using of acoustic redactors and specter analyzers, elaborated by other authors, in the following analysis of the data.

RESULTS

Low-frequency sounds accompanying the flight. The flight of moths causes aerodynamic swirls and acoustic waves with the frequency of wingbeats and its overharmonics. Disturbed airstreams form a turbulent trace of a flying insect (Brodskii, 1988), whereas low-frequency acoustic waves (in moth species studied, wingbeat frequency constitutes 30-50 Hz) spread radial from the source, strongly decreasing in the amplitude with the increasing distance.

Signals registered by a microphone situated above flying moths possessed distinctly non-sinusoidal shape, which is first of all associated with the complicated dynamics of wing movements. The low-frequency component of the spectrum of sounds accompanying the flight is composed of a series of overharmonics of the wingbeat frequency (30-50 Hz), with general tendency to decrease spectral density toward high frequencies. The number of distinct peaks in the spectrum was determined primarily by the stability of wingbeat frequency and usually constituted 12-17. The highest number of overharmonics in the spectrum (no less than 22) was registered in the moth *A. circellaris* (Fig. 1). The root-mean-square level of sound pressure of low-frequency waves produced by flying moths constituted 70-78 dB LSP at a distance of 6 cm from the insect body.

Measuring of variability of air pressure oscillations in the turbulent trace demonstrated that experimental insects continuously tried to maneuver. In oscillograms shown in Fig. 2, variations of oscillations, corresponding to wingbeat rhythms divided by two (Fig. 2*c*) or by three or five (Fig. 2*d*) are visible. Apparently, the formation of movement patterns with the characteristic realization time equal to 2 or more wingbeat periods is the basic feature of the motor program. In this connection, the effect of "multiple subdivision" observed during generation of the continual sequence of echolocator clicks, described by us (Lapshin, 1996; Lapshin and Vorontsov, 2000, 2005) should be mentioned. By contrast to the emission of clicks, however, maneuvers of experimental moths were characterized by not so high stability of the multiple rhythms.

Ultrasonic acoustic flashes. Together with low-frequency waves produced by flopping wings, the flight of the majority of moths is accompanied by short acoustic flashes. A complicated temporal structure was typical of such signals independently of their association with certain wingbeat stages. The click, seemingly a single whole in the interval corresponding to the wingbeat, was subdivided into two or several (up to four) components, being analyzed at shorter timescale (Fig. 3). Spectral characteristics of separate

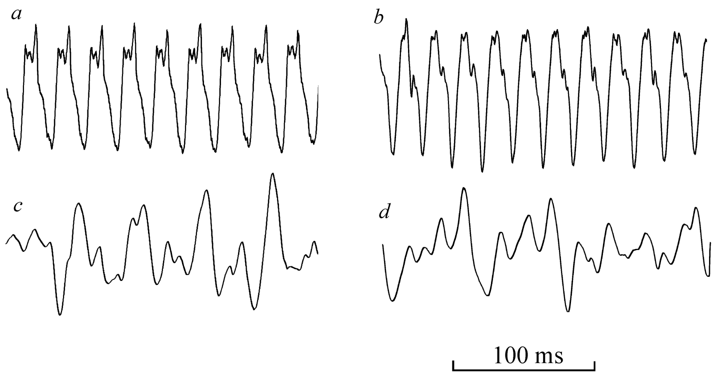

Fig. 2. Oscillogram of synchronous registration of sound pressure near flying moths: (*a*, *b*) low-frequency waves produced by flopping wings (microphone above the flying moth); (*c*, *d*) oscillations of sound pressure in turbulent stream, (*a*, *c*) *Agrochola macilenta;* (*b*, *d*) *Plusia festucae.*

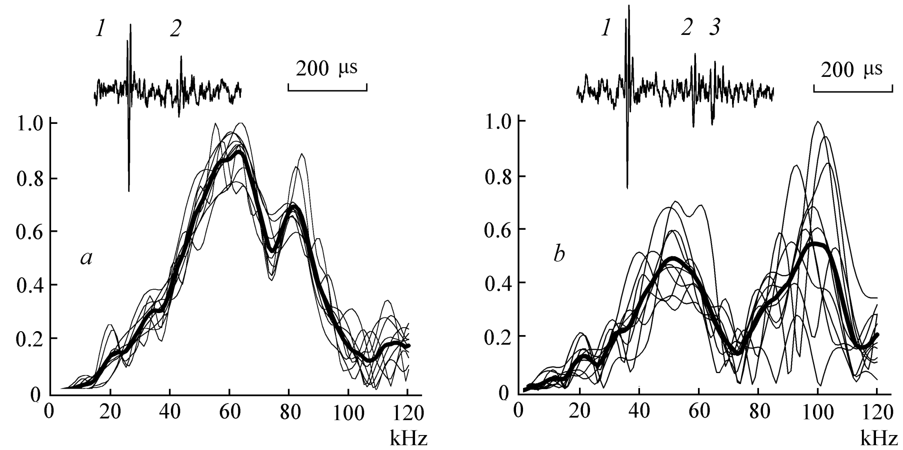

Fig. 3. Oscillograms and spectra of multiple sound flashes (*Amphipyra pyramidea*); (*a*) spectra of first impulses in a group (*1*); (*b*) spectra of second impulses in a group (*2*, *3*). Separated oscillograms was constructed according to the results of averaging of 10 spectra of clicks of the same type, preliminarily normalized by the amplitude. Abscissas: frequency; ordinates: degree of spectral components in relation to the maximum value.

components of such group could be either similar in their main features or significantly different. Alternation of single multiple flashes associated approximately with the same wingbeat stage was also observed during a single registration.

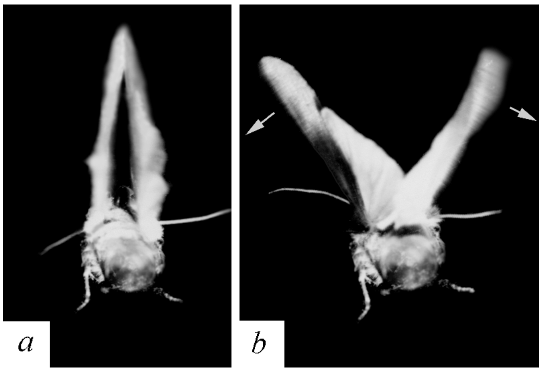

Fig. 4. Photographs of moths (posterior view) performed during registration of high-frequency acoustic flashes during upper wing position (*a*) during turning of the fore wing plains (*b*). The method of synchronized photography is described in the paper by Zhantiev et al. (1993).

The strongest spectral components of impulse flashes concentrated in the frequency diapason of 7-150 kHz. This tendency is characteristic of sounds accompanying the flight (independently of associations with certain wingbeat stages) and also of high-amplitude (more than 71 dB SPL) echolocator clicks. It could be assumed that similar tendency was retained in weaker signals with amplitude insufficient for wide-band measurements.

It would be rational to start the analysis of acoustic events observed during a single wingbeat cycle with the stage when moving moth wings occupy vertical position (Fig. 4*a*). In this moment, wing apices can touch each other, but such contacts are not necessary elements of the flight, because in some investigated specimens the interval between wings in this position still existed.

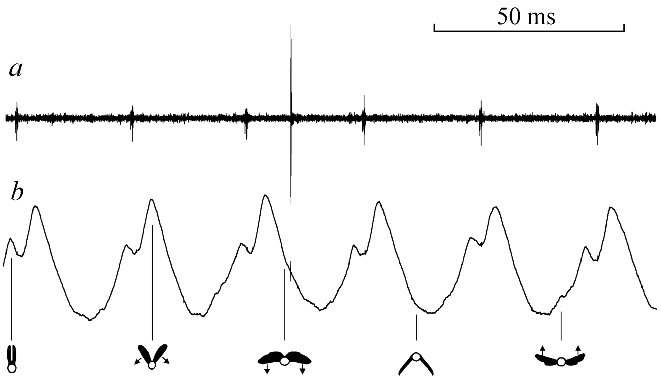

Fig. 5. Oscillograms of sounds waves produced by flying moth (*Amphipyra pyramidea*); (*b*) microphone is situated above the insect; (*a*) oscillograms of the same recording after frequency filtration in the band 10-120 kHz. The picture shows the scheme of wing positions in characteristic points of oscillograms; arrows indicate the direction of wing movements.

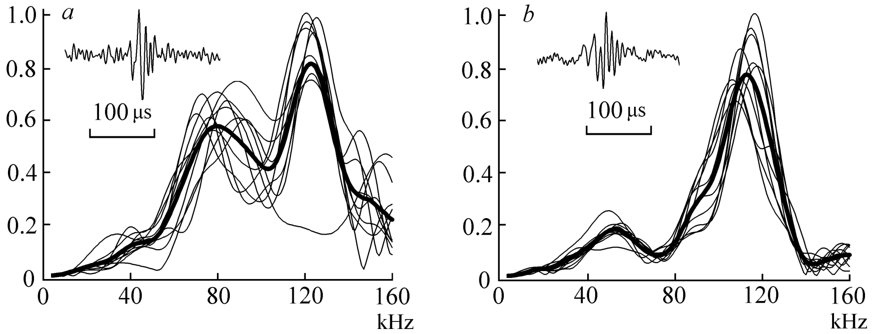

Fig. 6. Oscillograms and spectra of acoustic flashes associated with the stage of upper wing position of the moth *Xestia c-nigrum.* Simultaneous registration with two 0.25-inch microphones situated to the right (*a*) and above (*b*) the moth. Abscissas: frequency; ordinates: degree of spectral components in relation to the maximum value.

Moth wingbeats begin with the pronation (a strong turning of fore wing plains) (Fig. 4*b*). This process occurs so rapidly that we failed to observe it with the use of a stroboscope; it should be concluded that the duration of wing turning and of stroboscope flash is equal, constituting 2 ms. The local minimum corresponding to the jump of air underpressure is observed in the oscillograms of acoustic pressure (the microphone is situated above the moth) (Fig. 5).

During wing turning, solitary or, more frequently, groups of impulse flashes with the peak amplitude of 55-65 dB SPL (the most typical diapason of amplitudes) were usually registered with each wingbeat. Within these groups, clicks noticeably differed in the shape and spectrum (Figs. 3, 5); the amplitude of separate components varied from flop to flop from invisible level to 70 dB SPL. During a single 3 s accumulation seance, intervals between components could change from millisecond bits to several milliseconds.

Simultaneous measurements with two 0.25-inch microphones situated above and to the right of the experimental moth demonstrated that, during generation of the click in the stage of contacting wings, more high-frequency harmonics are emitted into the upper hemisphere more effectively (Fig. 6). As also follows from these results, variations in the spectrum of clicks associated with different wingbeat stages can be the result of different orientation of wing surfaces in relation to the recording microphone.

In moths, hind wing apices are, as a rule, closed during emission of impulse flashes; it gave Waters and Jones (1994) the reason to treat this emission as the result of contact between wing apices. However, in some specimens, it was evidently visible that during illumination of flying moths with a stroboscope synchronized with the moments of emission of such flashes, wings were situated closely to each other, but were not in contact (e.g., *E. paleacea* and *H. micacea).*

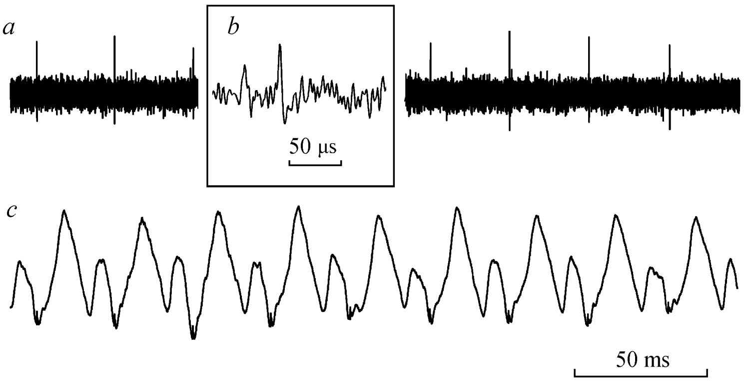

Fig. 7. Oscillograms of impulse flashes (*a*) and low-frequency waves (*b*) emitted during the lowest position of wings of the moth *Agrochola circellaris.* Fragment (*b*) shows two-component structure of the flash in shorter time scale.

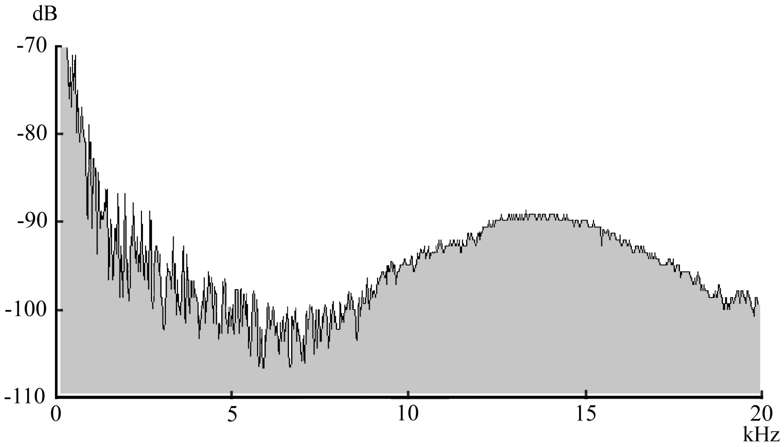

Fig. 8. Integral spectrum of noises produced by flying *Scoliopteryx libatrix* (microphone above the insect). Abscissas: frequency; ordinates: spectral density of sound pressure. The level of 80 dB (ordinates) corresponds to the spectral density of 5 x 10^{-6} Pa/Hz.

At the same time, some specimens, possessing visible contacts between wing apices, were flying so "silently", that no any high-frequency impulses were registered during their flight *(B. satura, B. amica, M. oxyacanthae, X. c-nigrum, S. libatrix, A. gamma, D. chrysitis, M. confusa,* and *A. circellaris).* These observations make a hypothesis on wing encounter as the original reason of clock generation doubtful.

In the lowest position, no wing encounter is observed; wing form an angle of 90-120° toward each other. In this stage, one more impulse flash, or, more frequently, several groups of flashes were observed in some specimens during each wingbeat (Fig. 7).

No direct correlation was revealed between ultrasonic emission and maneuvering of moths: flashes could possess very low amplitude at the background of active maneuvers and, by contrast, these flashes could be well expressed during the stationary flight.

Integral spectral characteristics of high-frequency sounds accompanying the flight. As a rule, the minimum was observed in the spectrum of the acoustic flow produced by the flying moth in the diapason from 3 to 5 kHz; spectral density in this zone was either comparable with the spectral density of self-produced noises of the microphone amplifier, or higher by several dB (Fig. 8). At higher frequencies, spectral density of accompanying sounds retained the stable level, occasionally sinuously decreasing with frequency. The use of a 0.5-inch microphone allowed tracing of the same tendency up to 35 kHz. The increase of the spectral density in the high-frequency component of the diapason was evidently associated with the development of ultrasonic flashes, timed with certain wingbeat stages. After removing of such flashes from records, the spectrum of modified fragments in the diapason higher than 2 kHz was virtually the same as the spectra of control recordings made without the moth in the sensitive zone of the microphone. Hence, it is evident that the level of the high-frequency component of the aerodynamic noise of the flight did not exceed the noise of the registering system (in the diapason of 2-20 kHz,

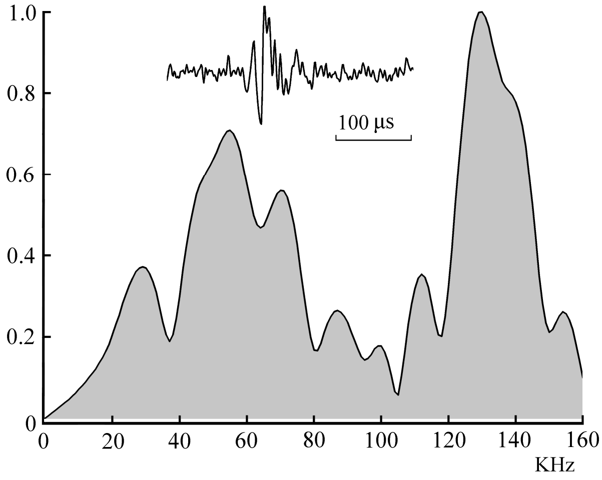

Fig. 9. Oscillogram and spectrum of echolocator click registered from the flying moth *Blepharita satura*. Abscissas: frequency; ordinates: degree of spectral components in relation to the maximum value.

root-mean-average level of self-produced noise of the microphone system constituted 18 dB SPL). This result is very important for the understanding of acoustic sensitivity of moths themselves.

High-amplitude clicks. Emission of high-amplitude clicks was more probably observed in two wingbeat stages: (1) when wings occupied horizontal position in their downward movement (Fig. 5), and (2) when wing occupied the same position during upward movements.

Measuring of physical parameters of high-frequency clicks showed the absence of significant differences in comparison with our earlier data (Lapshin and Vorontsov, 2000a), except for the signal spectrum. The use of a 0.125-inch microphone allowed registering one more peak in the diapason higher than 100 kHz; this peak exceeded more low-frequency components in the maximal spectral density (Fig. 9; peak amplitude of the click 82 dB SPL; position of wings during registration: horizontal, downward movement; the microphone is situated above the moth).

The results of the analysis of several registrations also confirmed the mechanism of generation of loud clicks, based on the breaking of clutching of fore wings with specialized areas of the metascutum (Lapshin and Vorontsov, 2000a): linked changes in the oscillograms of low-frequency component of the sound accompanying the flight, associated with wing braking by clutching mechanism, were observed during emission of such clicks.

Numerous observations demonstrated that moth can emit high-amplitude clicks virtually in any wingbeat stage. This circumstance significantly hampered subdivision of acoustic signals by the mechanism of their generation. The problem became even more difficult because of the partial overlapping of variability of amplitudes and spectra of clicks in all the species. Therefore, the reliable separation of types was possible only in cases, when peak amplitudes of clicks and the dynamics of their repetition significantly differed during several wingbeat periods (Fig. 5).

DISCUSSION

Mechanism of generation of high-frequency accompanying sounds. The analysis of numerous fragments of records of moth acoustic activity demonstrated that ultrasonic flashes with an amplitude lower than 65 dB SPL most probably appear in two wingbeat stages: in the uppermost position during the pronation and in the beginning of upward movement from the lowest position. It is clear that, in the second case, the generation of ultrasonic flashes cannot be explained by the encounter of wing apices; the position of wings excluded their direct contact. Such observations need another explanation of the emitting of impulse noises. Most probably, acoustic flashes appear in moths during the involution of wing surfaces (during pronation in the upper position and during supination in the lower one). Periodical turning of wings is the obligatory component of the flittering flight (Brodskii, 1988). Axial involution of the wing (a construction of the cellular structure) must lead to a cascade of rapid deformations associated with the loss of stability of the shape of structural elements composing wing surface.

According to this hypothesis, deformation of symmetrical wing areas will result in the appearance of clicks, separated by an interval constituting from millisecond bits (as a rule) to 1-2 ms in both wingbeat stages of the normal flight. Really, in our experiments, we repeatedly observed cases of generation of such paired flashes, but this phenomenon was not the absolute rule: the number of clicks associated with certain wingbeat stages could vary from 1 to 4 even in separate specimens (Fig. 3). In several cases, very high stability of inter-impulse intervals was retained in the sequence of paired or triple impulses; this phenomenon can hardly be explained within the frames of the hypothesis postulating their spatially independent emission. Hence, with a high degree of probability, some of the flash series recorded appeared during the cascade loss of mechanical stability of structures in one of the wings.

The examples of alternating of solitary and paired flashes associated with each wingbeat lead us to the conclusion that solitary acoustic flashes appear in moths during some certain flight regime, characterized by the asymmetry of the work of their wing apparatus. As follows from this conclusion, moths can fly actually "silently" in the ultrasonic diapason (i.e., high-frequency accompanying sounds will be lower than the noise of microphones). Actually, this conclusion is confirmed by our observations: in some experiments, moths did not produce any noticeable high-frequency impulses during visible encounter of wing apices.

On the whole, similarity of the spectral characteristics of the majority registered clicks point to the common character of structures emitting these sounds. Most probably, these structures are represented by proximal parts of wings.

Acoustic revealing of moths by bats. In order to minimize the probability of self-manifestation of the predator, bats decrease the loudness of echolocator signals or even pass to the passive location regime. Long-eared bats (*Plecotus*) use mainly audition during search for insects. In these bats, the length of the auricle exceeds the length of the body or is equal to the latter, which, naturally, determined the name of the group. The optimum of sensitivity of their auditory system is shifted to the low-frequency zone (Coles et al., 1989). Horseshoe bats (Rhinolophidae) also moved far forward in their masking technique: approaching moths, they sharply decrease the amplitude of echolocator signals or stop their emission at all, orienting exclusively by sounds produced by insects (Airapetyants and Konstantinov, 1974).

Experiments demonstrated that detection of a moth staying out of the zone of bat echolocation occurs from distances 6 m or shorter mainly according to "passive" location, i.e., localization of sounds produced by the victim itself (Sokolov, 1972). For these purposes, the detection of low-frequency components emitted by a flying prey is sufficient for prey finding. Now, it is hard to say anything certain on the role of high-frequency sounds, accompanying the flight, in these processes. Calculations made by Waters and Jones (1994) demonstrate that the amplitude of these sounds is too low for the detecting of moths by bats. In the pursuit stage, however, high-frequency sounds produced by flying moths can be crucial for the precise localization of the prey by the predator. In this connection, it should be noted that the problem of separation of external signals at the background of self-produced sounds is also relevant for bats.

The recently found by as effect of transformation of the frequency optimum of the acoustic perception in moths, linked with the emission of high-amplitude echolocator clicks, can be directly related to the question discussed (Vorontsov and Lapshin, 2002; Lapshin and Vorontsov, 2003a, 2004, 2005a). In these works, it was demonstrated that moths are able to modify parameters of their auditory system arbitrary; such transformations are provided by the activity of at least two mechanisms. Directly before the emission of a click, the auditory system of moths is "tuned" to one of the main spectral peaks of the anticipated echo (in the diapason of 50 kHz); then, the optimum gradually transforms, tuning to 15-20 kHz. The ability of moths to percept simultaneously very fine tonal signals (10-45 dB SPL) creates prerequisites for the detection of aerodynamic noises accompanying bat wingbeats. In this case, echolocator opposition of moths and predators can be "symmetrical" by acoustic characters of countcragents, i.e., not only bats, but also moths can detect a flying object by noises produced by the flight.

The ability of moths to use sounds accompanying the flight as **echolocator signals.** Acoustic impulses used by moths for the short-range echolocation possess the peak amplitude of 70-90 dB SPL (Lapshin et al., 1993; Lapshin and Vorontsov, 2005), i.e., by 3-30 times higher that the high-frequency sounds accompanying the flight (Fig. 5). At the same time, the real auditory sensitivity of intact moths allows detecting the echo from such "silent" acoustic impulses during space location at short distances (Lapshin, 2005). The question appears: do moths use the sounds of their own flight during echolocation?

Earlier, during investigations of the ability of flying moths to detect obstacles, it was shown that localization of the latter is possible at the background of clicks with an amplitude of 70 dB SPL or more, emitted by moths (Lapshin et al., 1993). In these experiments, when registered impulses were absent, experimental moths cquiprobably clashed against obstacles with different coefficients of acoustic reflection. On the basis of these results, we can conclude that weaker signals (i.e., not exceeding 70 dB SPL) were not used by moths during echolocation. However, it is not yet clear, whether this effect is associated with peculiarities of the certain experimental environment, or moths cannot detect the echo of noise signals because of their low amplitude, insufficient for turning-on of the regime of suppression of receptor reactions to the probing signal (Lapshin, 2005).

Influence of sounds accompanying the flight on auditory sensitivity of moths. Our investigations, performed as behavioral tests, demonstrated very high sensitivity of moths to ultrasounds; minimal thresholds of the reaction of intact moths constituted about 25-30 dB SPL for impulse signals and 10 dB SPL for tonal signals (Lapshin, 2005a). The reliable increase of the average frequency of emission of echolocator signals by moths was accepted as the criterion of the reaction threshold. It is clear, that real auditory thresholds of moths were evidently lower than estimations obtained. Thus, the peak amplitude of noise flashes exceeds auditory thresholds of moths by 40 dB (or by 100 times) or more. In intervals between flashes, the noise background produced by flying moths possesses the level comparable with the abovementioned self-noises of a 1-inch microphone (18 dB SPL), which is close to values of auditory thresholds.

Electrophysiological experiments with *A. perflua* demonstrated that the increase of the frequency of repetition of click stimuli by 2 times, from 30 to 60 s, resulted in the partial suppression of the reaction of A_1 receptor of the tympanal organ (Lapshin, 2005a). Simultaneous action of noise flashes accompanying each wingbeat and rhythmical external signals is equivalent to the increase of the average temp of stimulation of the auditory system. Such increase in frequency had to lead to the suppression of auditory receptors response and, correspondingly, to the increase of thresholds. However, acoustic thresholds measured in intact moths were significantly lower that those obtained in electrophysiological experiments. Significant increase of the auditory sensitivity in combination with the independence of measured values of thresholds from flight noises of experimental moths (Lapshin and Vorontsov, 2000) can be explained by the dynamic tuning of thresholds in receptors of the tympanal organ to the stereotypical "profile" of the noise, accompanying each wingbeat (Lapshin and Vorontsov, 2005a). Naturally, this hypothesis means, on the one hand, functioning of highly effective system of regulation of auditory receptors in the central nervous system of moths and, on the other hand, the presence of specific 'low-noise' temporal periods in each wingbeat.

Processes of dynamic transformation of auditory receptor parameters in correspondence with the input noise are most likely special cases of the more general phenomenon. In animals, including insects, the system of filters must function at all the stages of the analysis of the received information; the goal of these filters includes preventing of receiving of sensory signals associated with self-movements and activity (auto-noises) influence by the central nervous system. High degree of correlation with the rhythm of animal movements is one of the main characters of auto-noises.

As for as all the moths possess their individual peculiarities, after the emergence into adults, their wings gradually loose their original properties. The functioning of the tuning system to self-produced noises must be constantly optimized, taking into account the individual dynamics of the noise flow. Our data, demonstrating that auditory thresholds of *A. pyramidea* moth gradually decreased from 65 to 34 dB SPL at a frequency of 50 kHz (Lapshin and Vorontsov, 2000) can serve as an indirect confirmation of this hypothesis. We can assume that this tendency to shift the thresholds reflects the process of organization of the system of separation of external signals from self-produced noises of the flying moth.

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