

# Ways of Developing Acoustic Signals in Birds

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**Abstract**—An analysis of Russian and foreign literature data on the ways of developing acoustic signals in birds is presented. The physical analysis of acoustic signals is given for six species of birds: long-tailed skua (*Stercorarius longicaudus* Uicill), herring gull (*Larus argentatus* Pontopp.), sabine's gull (*Xema sabini* sab.), curlew sandpiper (*Calidris ferruginea* Pantopp.), red-throated diver (*Gavia stellata* Pontopp.), and black-throated diver (*Gavia aterica* L.). Signals of embryos, baby birds, and adult birds are considered. The denervation of the syrinx in baby and adult birds was investigated to obtain a pattern of generation of acoustic signals in the absence of syrinx innervation. The temporal-frequency signal characteristics are compared to those of decapitated birds. The examples of acoustic signals of these birds confirm the significant role of the physical characteristics of morphological structures participating in the generation of acoustic signals in birds.

**Keywords:** acoustic signal, syrinx, denervation, decapitation, frequency analysis

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## INTRODUCTION

Initially, the structure of an acoustic signal in birds is determined by the morphological structures that form it. This is true for signals generated by the respiratory system of birds and nonmechanical signals formed as the result of hitting an object with the beak or the friction of separate body parts against each other. The original sounds of all bird species were similar. External conditions of species have changed over the course of evolution and affected the structure of acoustic signals, which both determine identification of species and convey individual information. It is known that identification of species provides the necessary insulating mechanism responsible for species' survival. Individual deviations provide for the maintenance of resistance of a reproductive pair protecting their territory and food.

In conditions of competitiveness, each species possesses a group of signals reflecting the emotional state caused by an alarming and catastrophic situation. These signals must be understandable for any neighbor species and thus, be similar. Their structure must allow for the distance of transmission, which determines certain physical parameters of a signal.

To understand the development of acoustic signals in birds, we analyzed the structure of birds' signals beginning from the egg, especially in nonpasserines, as an original signal in the development of the species and, probably, reflecting its original development. Initial regulation of the signal-generating apparatus, the syrinx, is significant for the development of a signal. We attempted the reconstruction of a signal structure without nervous regulation using the methods of syrinx denervation. Some data have been obtained during the decapitation of birds, when the structure of a signal

is determined only by the mechanical parameters of the trachea.

Nevertheless, it is important to elucidate the physical structure of alarm and disaster signals in different species, because it is probable that the oldest signals, which were not affected by significant changes, and their structure are identical in different species.

## HISTORY OF THE DEVELOPMENT OF ACOUSTIC SIGNALS IN BIRDS

Principles of coding and transmission of biological information as acoustic signals in birds are the key factors in investigations of the mechanisms of communication and regulation of their behavior. General mechanisms of acoustic signal generation in the inferior larynx of birds and the related spectral-time structure of the studied signals can serve as a first step in investigation. Analysis of the acoustic structure of signals and larynx structure in early ontogenesis allowed the identification of some regularities of phonation in birds during this period and consideration of their age-related changes [10]. It was determined that the frequency modulation curve in the acoustic signals revealed in the early ontogenesis of birds is characterized by a somewhat bell-shaped sonograph, independently of taxonomic adjunction and type of individual development. Further changes of modulation type must be considered a result of the involvement of nervous regulation of syrinx muscles. Nervous regulation in passerines occurs through the left branch of the hypoglossus nerve. Solely right-side laryngeal denervation results in disturbance of respiratory functions [18, 21]. The variety of morphological types of syrinx represented in different taxonomical groups of birds

[8] presupposes the presence of various levels of vocalization regulation in these groups. The groups with a low number of vocal muscles are especially interesting. This number differs significantly for various groups of birds and generally correlates with voice development [7]. The primitive syrinx is formed by the trachea with numerous cartilaginous rings, with or without a weak semilunar fold. There are 1–2 syrinx muscles, or they are significantly reduced [8]. It can be assumed that taxonomic groups of birds with the primitive type of syrinx maintain the “baby bird” type of acoustic signal generation, i.e., without significant nervous regulation of the tension of the syrinx muscles.

In this regard, the general scheme of acoustic signal generation in the inferior larynx of birds as it is currently known was investigated [14, 26]. Air passing through the inferior larynx stimulates internal tympanic membranes. Membrane tension is provided by internal and external voice muscles. The inferior larynx is indirectly affected by *m. tracheolateralis* and *m. sternotrachealis* [8]. These become functionally mature by the time of hatching and can provide the permanent tension of internal tympanic membranes. With equal and simultaneous tension of the membranes (each of which can serve as a sound generator), the frequency of the signal in both generators becomes equal. As a result, frequency modulation becomes bell-shaped or close to it. The degree of manifestation of this modulation type can be determined by the velocity of air passing through and alterations in membrane tension during sound generation. The bell-shaped form of frequency modulation is specific for early signals of embryos and young baby birds in almost all groups of birds including passerines, and it is maintained in definitive signals in numerous groups of nonpasserine birds [10, 12]. In some groups of birds, piercing of the shell membrane of eggs and stabilization of pulmonary breathing of embryos result in sharp changes in the spectral structure of generated signals [10]. The transition to generation of noise or broadband signals with insufficient frequency modulation is specific to birds with the primitive type of inferior larynx structure. Vibration of vocal labia can serve as the source of amplitude modulation and resonance events in the trachea, and accessory cavities as a source of formants [26]. However, respiratory acts with a certain intensity are a required condition.

#### SOME RESULTS OF OUR OWN INVESTIGATIONS

Voices of the following bird species were recorded: long-tailed skua (*Stercorarius longicaudus* Uicill), herring gull (*Larus argentatus* Pontopp.), sabine's gull (*Xema sabini* sab.), curlew sandpiper (*Calidris ferruginea* Pontopp.), red-throated diver (*Gavia stellata* Pontopp.), and black-throated diver (*Gavia aterica* L.). More than six specimens of every species were registered,

including embryos. Sonographic analysis of 40 signals was carried out for every species and every age group.

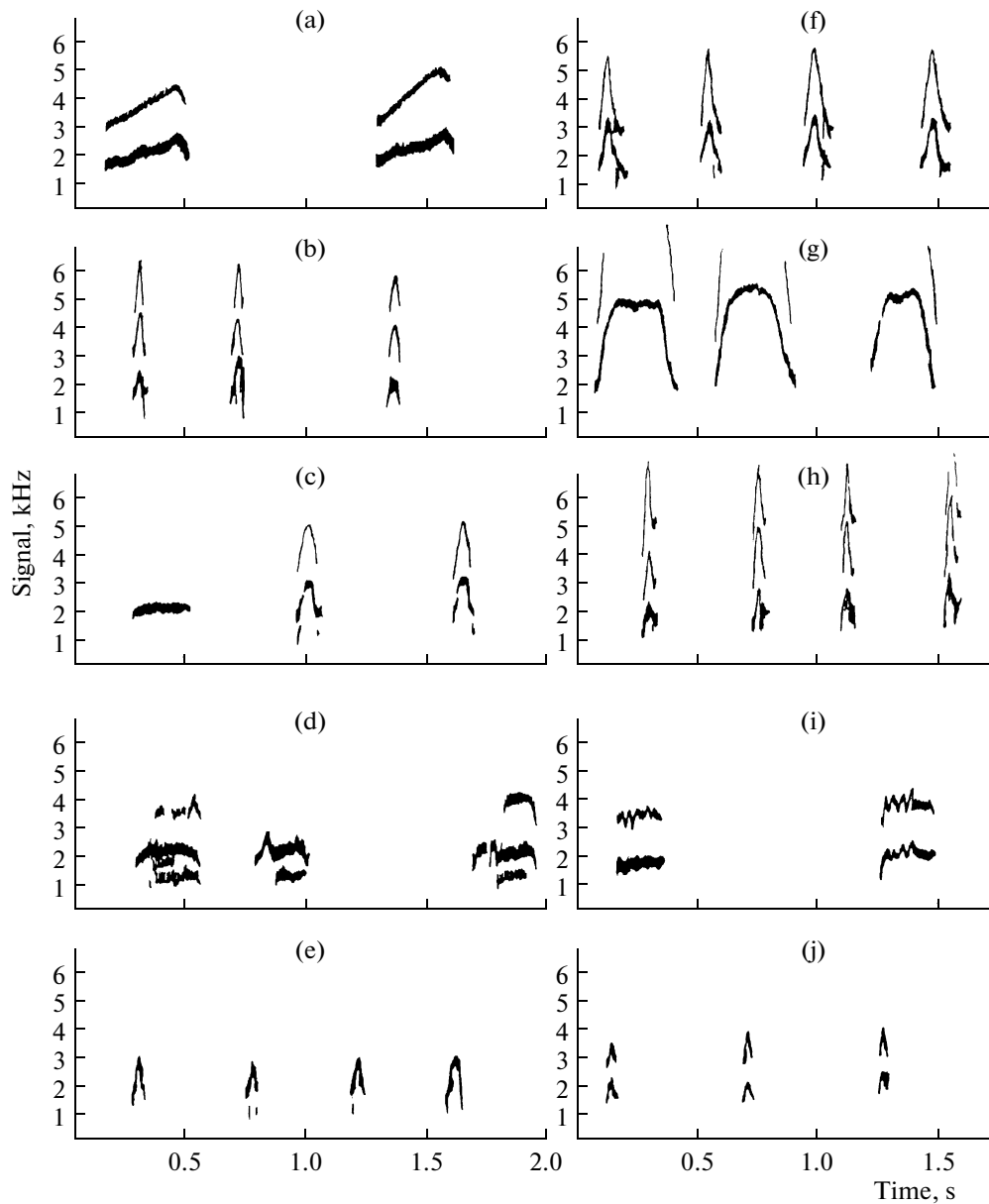
Three variants of denervation of the inferior larynx were used: left-side, right-side, and bilateral. Branches of the sublingual nerve were cut according to the method described in previous work [1].

Figure 1 shows the signals of embryos of two species: red- and black-throated divers. Figure 1a shows the structure of the acoustic signal of red-throated diver embryos recorded three days before hatching. In comfortable conditions, the respiration frequency of the embryo is normal, and signals formed during respiration correspond to the possibilities of the morphological structure of the acoustic system in a biological object. In this case, these signals fall in the frequency range of 1.5–5.0 kHz and are represented by two harmonics. The duration of a single signal is 0.3 s; the frequency of the general harmonic increases from 1.5 to 2.7 kHz in 0.25 s and falls to 1.7 kHz in 0.05 s. This acoustic signal structure corresponds to simple air perflation with a certain pressure through a tube that appears during embryos' respiration. This signal of red-throated diver embryos (Fig. 1g) differs in the frequency range of the first harmonic, which is located in the range 1.3–5.5 kHz, and in its bell-shaped form. These deviations indicate the possible diversity of embryonal signals in comfortable conditions and the flexibility of the acoustic system, although these deviations indicate the similarity of such signals when they are similar in duration and simplicity of structure.

When embryos of both species of birds are in uncomfortable conditions, cooling, in our case, the character of changes in signal structure is regular (Fig. 1b). Each signal dispatch is shortened to 0.1 s and characterized by a sharp increase of frequency. The range of frequencies increases and falls within 0.8–6.1 kHz. This change in the structural dynamics of a signal is caused by the need to increase their informativity and distance, which is related with conditions of survival. However, the structure of these signals remains primitive and bell-shaped, appearing during simple air perflation through a tube, though much more frequently than in comfortable conditions.

This structure remains in both species, even when the bird pecks through the egg (Figs. 1c, 1h). Probably, the degree of discomfort is expressed as an increase in signal rhythm (Fig. 1h), and a signal distorted while passing through a hole in the shell was visible in the beginning (Fig. 1c). This is confirmed by the structure of signals, which were recorded directly through a hole in the shell (Figs. 1d, 1i).

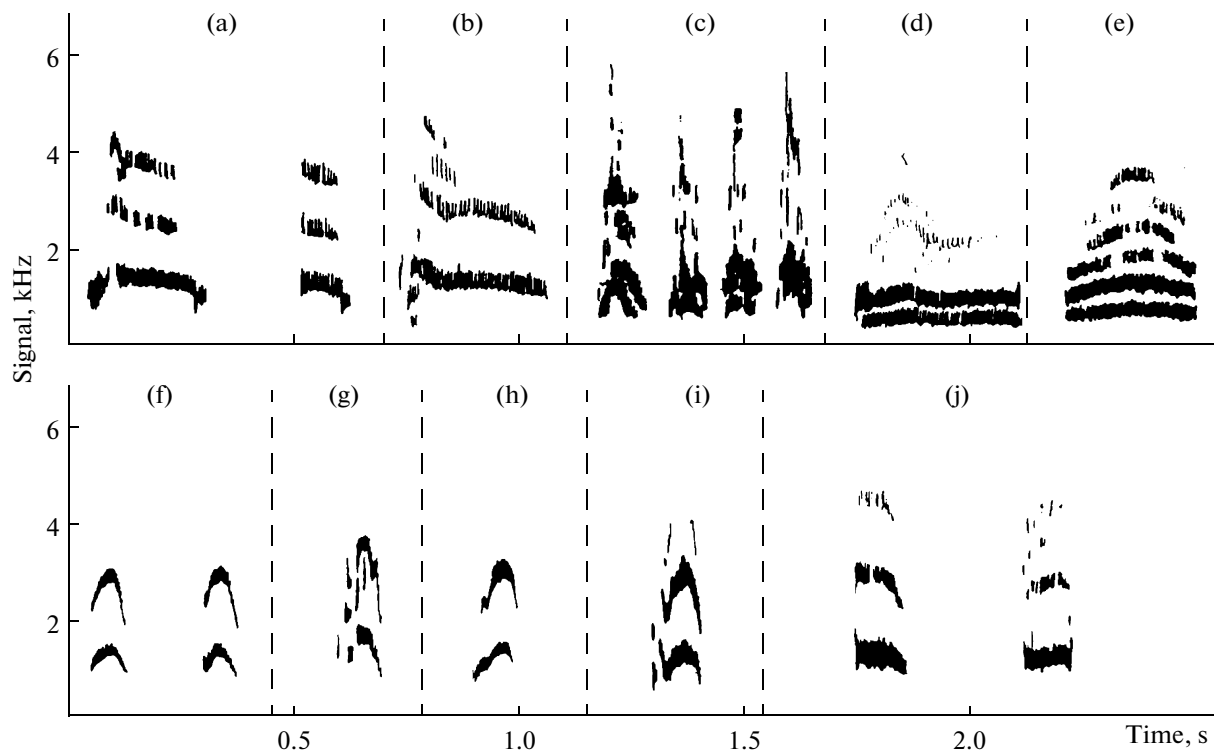
Feeding signals of 2- and 3-day-old baby birds (Figs. 1e, 1l) are specific in their structure. It is clear that these signals are specifically bell-shaped with higher rhythmicity, compared with the comfort signals, but the frequency range is 1.2–3.0 kHz, which is significantly higher than the discomfort signals.



**Fig. 1.** Sonograms of acoustic signals of black-throated diver (*Gavia aterica* L.): (a) signal of embryo at rest, (b) discomfort signal of embryo, (c) signal during pecking through shell, (d) groaning signal of two-day-old baby bird, (e) food signal of two-day-old baby bird; red-throated diver (*Gavia stellata* Pontopp.): (f) discomfort signal of embryo, (g) signal of embryo at rest, (h) signal during pecking, (i) groaning signal of two-day-old baby bird, (j) food signal of two-day-old baby bird.

A comparison of the voice characteristics of adult species of herring gull (*Larus argentatus*) in different functional states is shown in Fig. 2. Figure 2a shows the roll-call signal of a flying herring gull pair. The signals split into three harmonics with the main frequency of the first located near 1.5 kHz. Signals of the male and female differ in duration and are characterized by the general structure of signal composition. In the case of danger, one of the pair sounds the alarm signals, one of which is shown in Fig. 2b. Its structure differs from the species signal by increased duration

and time discrimination that is serrated in form. This alarm signal structure is universal for numerous species of birds and allows communication between species, which is important in dangerous situations. In addition, the serrated signal allows its distribution over long distances. Finding a source of danger, a gull sounds a signal of aggression, shown in Fig. 2c. Its structure is different from that of previous signals. The shape of a single signal is joined by a bell-shaped signal with numerous harmonics, with the main harmonics located in a frequency range similar to that of species-



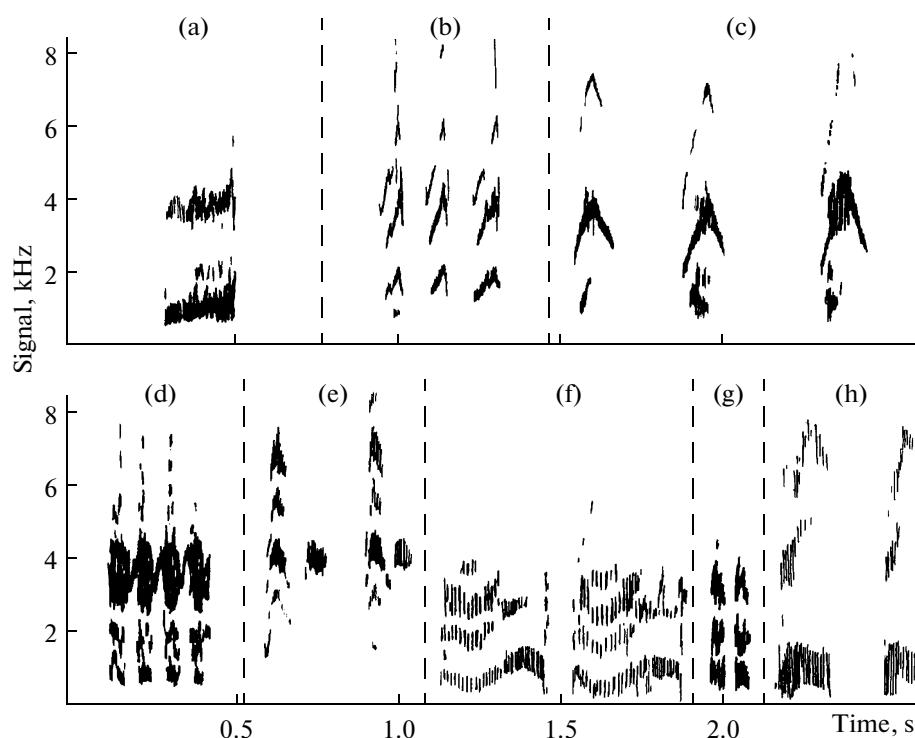
**Fig. 2.** Sonograms of acoustic signals of herring gull (*Larus argentatus* Pontopp.): (a) signals of two birds in flight, (b) alarm signal in flight, (c) signal of aggression in flight, (d) signal with bilateral denervation of syrinx, (e) signal of decapitated bird; long-tailed skua (*Stercorarius longicaudus* Uicill): (f) signal in flight, (g) alarm signal in flight, (h) signal with bilateral denervation of syrinx, (i) signal with incised trachea, (j) signal of decapitated bird.

specific signals. The function of aggression is determined by the frequent appearance of this structure in time. These facts indicate that a simple structure signal similar to that of embryos is the basis of these signals.

It is important to observe the signal of this species with double-sided denervation of the syrinx (Fig. 2d). In this case, the signal is released from nervous regulation, which is clearly expressed in species signals and the alarm signal. Since this signal was recorded in hands, it is an alarm signal in certain situations and its duration and internal structure are similar to those of alarm signals in natural conditions. The deviations are clearly expressed in the general signal frequency. This frequency is significantly lower than the one found in species signals of gulls and is located in the region of 0.5 kHz. The second harmonic without modulation corresponds to the first and resembles a monofrequency. The signal formed after pressing on pneumatocysts during the decapitation of birds is most interesting (Fig. 2e). In this case, signal duration is determined by the duration of pressing, and the frequency range is determined by morphological structures, in particular the length and diameter of the trachea. It is clear that the main frequency remains similar to the frequency under bilateral denervation, and the number of additional harmonics increases as a result of

strong pressing on the pneumatocysts and, thus, stronger air perflation through the trachea.

Another situation was observed in the structure of acoustic signals in long-tailed skua *Stercorarius longicaudus*, which are shown in Fig. 2 (f–j). The species signal of long-tailed skua in flight is a bell-shaped primitive signal consisting of two harmonics. The alarm signal (Fig. 2g) is slightly similar to the species signal; however, according to all rules of alarm signals it is disrupted in time, which corresponds to its functional purpose. Under bilateral denervation of the syrinx (Fig. 2h), the signal structure hardly differs from that of the species signal (Fig. 2f). This indicates that the species signal of this species remains at the level of forming simple signals that are specific for baby birds' signals. This signal repeats the structure of an alarm signal (Fig. 2g) upon simple cutting of the trachea (Fig. 2i). Upon decapitation of long-tailed skua, we observe the natural physical process of air perflation through the trachea in one direction, when the bell-shaped structure of the signal disappears (Fig. 2j). The signal becomes monofrequent, similar to the above-mentioned signal obtained after decapitation of herring gull (Fig. 2e). Deviation in the duration of signals is a result of different duration of pressing on pneumatocysts.



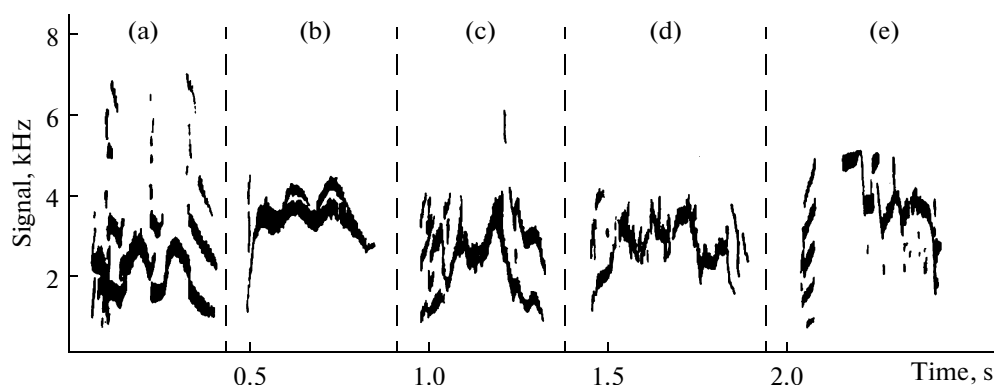
**Fig. 3.** Sonograms of acoustic signals of curlew sandpiper (*Calidris ferruginea* Pantopp.): (a) invocatory signal, (b) alarm signal, (c) signal of decapitated bird; sabine's gull (*Xema sabini* sab.): (d) signal of two-week old baby bird, (e) species signal of adult bird in flight, (f) alarm signal in flight, (g) signal of aggression in flight, (h) signal of decapitated bird.

Some signals of curlew sandpiper *Calidris ferruginea* (Figs. 3a–3c) were considered in order to compare them with those of the herring gull *Larus argentatus* and long-tailed skua *Stercorarius longicaudus*. Figure 3 shows a species invocatory signal of males seeking to attract females. It was noted that the main frequency of the first harmonic is located in the range from 0.5 to 2.0 kHz, and there is a second harmonic. Signal duration was 0.2 s. This signal is serrated in form with a rise in the main frequency from the beginning of the signal to its termination. Another alarm signal structure (Fig. 3b) was observed, whose shape was specific for alarm signals of a majority of birds [4]: short dispatches (approximately 0.05 s) in a broad range of frequencies (from 1.0 to 8.0 kHz) with repetition frequency equal to length of dispatch. It was noted that broadband and frequent repetition of dispatches provides for a signal's long range and interspecies communication. This resemblance in different species can be explained by the simplicity of reproduction of this signal for any acoustic morphological structure and, thus, by its ancient nature. The signals of decapitated birds confirm this explanation (Fig. 3c). As the repetition frequency of dispatches is determined by the frequency of pressing on pneumatocysts, this parameter was not considered. The structure of a dispatch was also considered. While dispatch structure in the herring gull and long-tailed skua was monofre-

quent, it was bell-shaped in the red-throated diver, which completes the picture of the initial signal in different birds and allows one to speak of the diverse origin of the initial signals of birds.

The range of investigated species was broadened and single signals of sabine's gull (*Xema sabini*) were considered (Figs. 3d–3h). Figure 3d shows the specific disaster signal of a 2-week-old baby bird. Pronounced broadband (from 0.8 to 7.5 kHz) combined with a dense and continuous sequence of single dispatches 0.05 s in duration is characteristic in structure for different adult species and baby birds.

The species signal of sabine's gull consists of two different dispatches: broadband in the range 1.5–8.0 kHz and monofrequent at 4.0 kHz. This structure is probably specific for this species, bearing individual features. If a bird encounters danger, it sounds the alarm signal (Fig. 3f) in flight. This signal is serrated and frequently repeats with an interval of 0.1 s in different species of birds. Signals of aggression or disaster were also considered (Fig. 3g). A structure characteristic of signals of a majority of birds was observed. A signal of a decapitated bird was additionally considered (Fig. 3h). The duration of single dispatches and intervals between these were not considered, as these are determined by artificial pressure on pneumatocysts. By its structure, this signal is an average between



**Fig. 4.** Sonograms of acoustic signals of two-day-old baby herring gull (*Larus argentatus* Pontopp.): (a) alarm signal, (b) signal with bilateral denervation of syrinx, (c) signal with left-side denervation, (d) signal with right-side denervation, (e) alarm signal of one-month-old baby bird.

similar signals of the herring gull and red-throated diver. A first harmonic with a frequency of 1.5 kHz and three upper harmonics are the basis of this signal. It differs by time discrimination, which was absent in previous species, and its form is an average between a monofrequent signal as in the herring gull and a bell-shape as in the red-throated diver. This can be considered a third shape of possible generation of acoustic signals formed upon free air perflation through the trachea. This diversity can appear under different dynamics of the passing of air through a morphological structure like the trachea in birds.

The influence of nervous regulation of the syrinx on the structure of acoustic signals in a 2-day-old herring gull was considered (Fig. 4). Alarm signals of the baby bird were analyzed. Figure 4 shows the complex structure of the signal located in the range from 0.5 to 7.0 kHz. This signal is a combination of bell-shaped dispatches transformed into each other, which was observed in signals of the rest of the embryos shown in Fig. 1. The signal also underwent insignificant changes in the case of left-sided and right-sided (Fig. 4c and 4d, respectively) denervation of the syrinx. The structure of the signal upon bilateral denervation was generated in the acoustic system of a 2-month-old baby bird in the absence of nervous control. The signal was similar to warbling with a pronounced general frequency (approximately 4.0 kHz) and the same duration as in the case of denervation of the syrinx. Thus, we have obtained another shape of the simplest signal, which can be considered as initial in the development of acoustic signals in birds.

## CONCLUSIONS

At present, it is known that muscles of the respiratory and vocal systems in birds function synchronously [23], and the regulatory mechanism of respiration and acoustic signal production is related with the nucleus

of *n. intermedius* [24]. Thus, the results of our experiments indicate that denervation of the syrinx in baby birds in the considered groups did not affect the processes of nervous regulation of tension of the tympanic membranes, though it influenced respiration. Considering the fact that a similar regularity occurred upon denervation of the syrinx in adult birds, it is correct to view the role of nervous regulation of membrane tension as limited. This indicates the primitiveness of the acoustic process in the considered group of birds.

The spectral-temporal structure of disaster signals of passerines (amplitude-modulated, broadbanded warbling) is achieved by the generation of sounds upon maximal exhalation. The increasing velocity of the passing air and its volume cause an increase in signal duration and the warbling character of the sound [25]. The protective reactions of birds, especially in dangerous situations, are the most primitive and innate form of behavior. The danger signals belong to the most ancient group of signals, and the mechanisms of their generation were probably maintained during evolution without changes in the majority of birds, independently of taxonomic affiliation.

It was determined for nonpasserine birds that dissection of the right and left branches of *n. hypoglossus* in both 1- to 3-day-old baby birds and adult species causes changes mostly in the time structure of sounds. It was determined that such change in the structure is a result of disturbance of respiratory function.

Nervous regulation of the syrinx in passerine birds occurs through the left branch of *n. hypoglossus*, whereas dissection of the right branch disturbs only respiratory function and does not influence the general picture of birds' warbling [1, 22].

Bilateral denervation of the lower larynx in both passerine and nonpasserine birds does not result in significant changes in the structure of alarm signals [2, 3]. The duration of alarm signals usually increases upon denervation of the syrinx, which is determined by the

disturbance of respiratory function. It was determined that denervation of the syrinx in nonpasserine birds does not affect the nervous regulation of tension of the tympanic membranes and insignificantly affects respiration.

All changes in the spectral structure of acoustic signals upon denervation of the syrinx in nonpasserine birds are the result of disturbance of respiration. Although passerine birds are characterized by a multi-muscular inferior larynx, stabilization of the control of tension of the tympanic membranes probably occurs gradually in ontogenesis [9, 11]. The absence of significant changes in alarm signals upon denervation of the syrinx in passerine birds allows the supposition on the absence of a regulated acoustic process, as compared with warbling and several sound signs [22].

Thus, the initial "baby bird" type of acoustic signal remains in passerine birds during alarm signaling, as in nonpasserines. All changes in the spectral structure of signals during this type of acoustic signaling and denervation of the syrinx can be explained by respiratory dysfunction but not dysfunction of nervous regulation [2]. Analysis of the acoustic signal system of passerines showed the variety of complex forms of frequency modulation in several signals and warbles. This is undoubtedly a result of activity of the developed muscles of the syrinx and its nervous regulation. Thus, the primitive type of acoustic signals, occurring without sufficient nervous regulation of the syringial muscles, is represented in passerines at the earliest stages of ontogenesis and is maintained without changes in some special signals (for instance, in alarm signals).

It should be noted that similar regularities are specific for acoustic signal systems of several reptiles, in particular in crocodiles [16]. The structure of squeaks of baby birds is sufficiently close to the sounds of embryos and young birds, and the sounds of adult crocodiles are similar to the acoustic signals of birds with the primitive type of inferior larynx. Several features of the inferior part of the trachea in crocodiles are similar to the syrinx of birds [8].

Probably, the ancestors of birds were characterized by acoustic systems similar to that of crocodiles. The reptilian type of acoustic signals was inherited to some degree by birds. The ancestral, initial type of acoustic signals is specific for all birds at the earliest stages of ontogenesis, independently of their taxonomic affiliation and peculiarities of individual development. This is maintained in definitive signal systems in the majority of groups of nonpasserines with the primitive type of inferior larynx and in most ancient forms of signals (alarm signals) in passerines.

Voice and hearing developed simultaneously and independently along the general line of evolution of birds leading to passerines [7]. The great number of adaptive parallelisms [5] is a specific feature of evolution of the auditory system in birds. The fact that the adaptive variability of the acoustic apparatus within separate groups can repeat the stages of evolution of

the acoustic system of birds is an important peculiarity of the parallelisms [6].

An increase in the velocity of passing air and its volume achieved on acoustic signal generation upon full exhalation in conditions of absent or weak nervous regulation (signals of discomfort and food signals in the maximal phase of food reaction of baby birds) determines their broadband, amplitude- or frequency-modulated structure. This type of acoustic signaling is maintained in adult passerines in the ancient form of signals as alarm signals. Thus, their spectral-time structure is sufficiently close to the structure of baby bird signals indicated above.

Greenwalt [13] in his first analyses of the generation of sounds by birds posited the independent and simultaneous production of sounds from both parts of the syrinx. The mechanism providing production of these sounds was experimentally investigated by Larsen and Goller [17]. The frequencies of vibrations of syringial structures were evaluated using a detector of optical vibrations. It was determined that the vibrations correspond to signal production. In the opinion of the authors, this confirms the participation of these structures in sound production. The recent studies of French researchers confirmed these results and showed the simultaneous double generation of sound by the larynx in king penguins [15, 19, 20]. This results in the appearance of a high number of harmonics in the signals of baby birds, which provides for the reliability of their individual recognition. This combination within a short signal can be explained by the mathematical theory of information, which states that the informational abundance of a signal facilitates its recognition in the noisy conditions of a communicative channel. King penguins communicate with their young in such conditions.

The considered examples of acoustic signals of decapitated birds confirm the key role of physical parameters of the morphological structures involved in signal generation.

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