

GEOGRAPHICAL VOICE VARIABILITY IN ANIMALS AS AN ECOLOGICAL
AND EVOLUTIONARY PROBLEM

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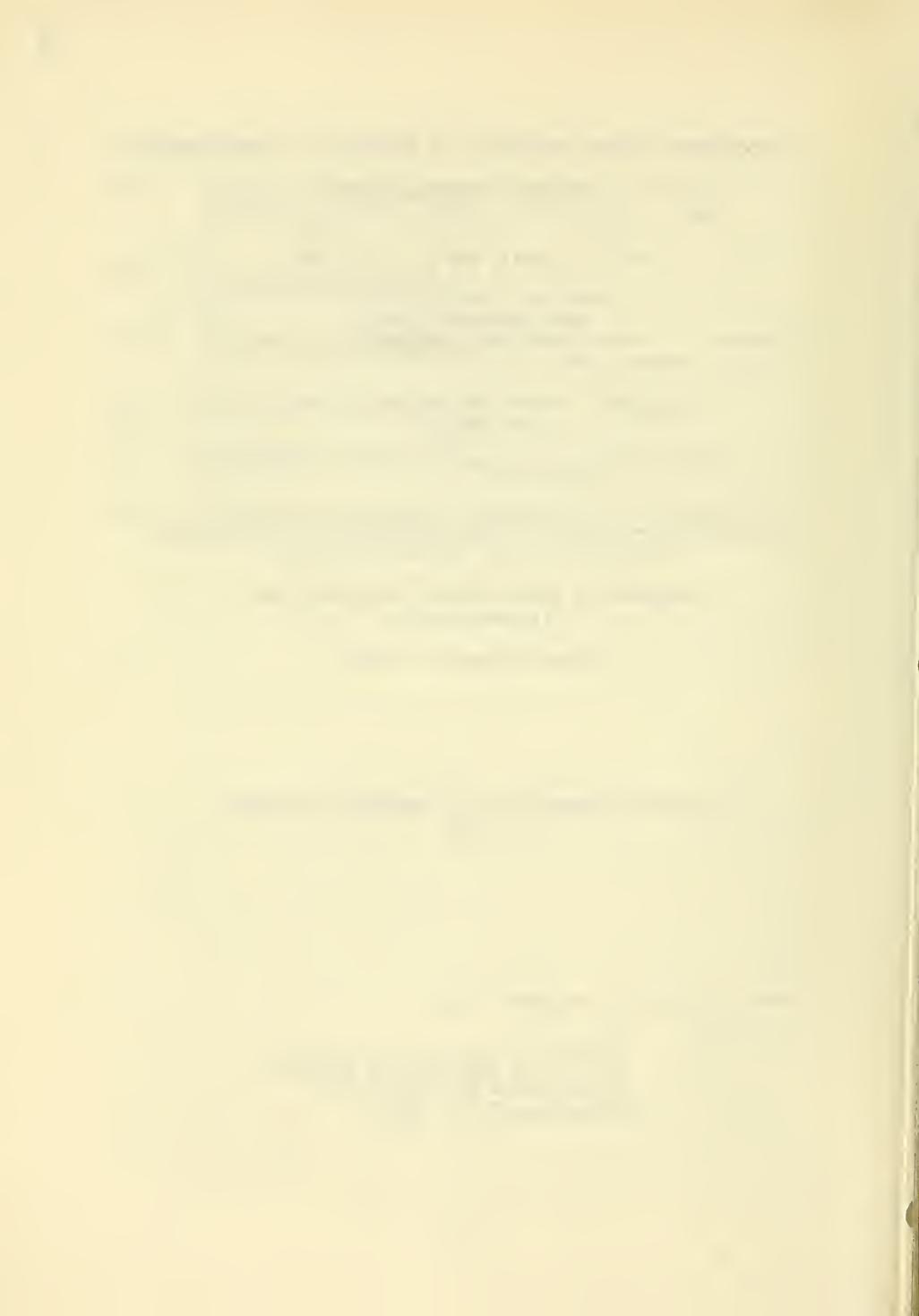
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The problem of geographical voice variability in animals is far from new. The great increase of interest in this field in our time can be laid to the development of complex physical, physiological and ecological investigations, which have transformed bioacoustics from an unsophisticated 19th century field of study into a modern, clearly defined science with its own problems, tasks and methods of investigation.

In regard to the practical applications of bioacoustics, the two following branches are developing rapidly: bionics and studies concerning the factors affecting the behavior of animals. In both cases the geographical aspects of bioacoustics find wide application.

Regarding bionics, bioacoustics provides material concerning the means employed by animals for coding and communicating vocal information under specific environmental conditions and concerning the dependence of vocal communication on noise and interference against the background of "sound environments," the biotope, etc. Regarding the investigation of the factors governing the behavior of animals, bioacoustics contributes valuable information on the specific aspects of the vocal signals of various territorial (interspecific and intra-specific) groupings of animals. These signals often lose their universality because of the development of "local information codes." The discovery and investigation of "local dialects," and the wide use of recorded voices to frighten off predatory animals, have directed special attention to the study of the geographical variability of the mechanisms of vocal communications.

The development of the theory of communication between animals (Sinnott, 1961; Frings, 1962; and others) is an important contribution to the above fields of study. The development of the science of ecology, especially in its geographical and evolutionary aspects, had a considerable influence on the formation of the theoretical bases of bioacoustics. Here the following kinds of investigation should be differentiated: the study of populations, landscape ecology, general ecogenesis, and ecological-geographical isomorphism.

All this has led to the following situation: the old theories and reviews - as found, for instance, in the excellent works of F. Groebbel, 1925; C. Witchell, 1896; O. Heinroth, 1924, and other workers - have become outdated. In the meantime the new data which

have been accumulating remain unprocessed. The introduction of mechanical instruments for sound recording and sound analysis into the study of bioacoustics has brought present-day research to a level far above that of previous work. Present-day data arouse the interest of biologists of the widest variety: evolutionists, ecologists, and also specialists in the field of acoustic bionics. The problems of communication and mechanisms for coding and communicating vocal information under specific environmental conditions thus acquire general biological interest and significance.

From the time at which the early works of N. I. Dergunov (1925) and A. I. Promptov (1927) appeared, the problems of local dialects and geographical voice variability in birds have been intensively studied in the USSR (Promptov, 1930; Kistyakovskii, 1958; Mal'chevskii, 1958, 1959, 1963; Dement'ev and Il'ichev, 1963; Simkin and Il'ichev, 1963; and others). In addition to these investigations, the following original works are of great interest: A. N. Promptov, 1944, 1956; A. N. Promptov and E. V. Lukina, 1945. These works deal with the mechanisms of the above phenomena.

At the end of the 19th century, the problem of geographical voice variability began to be studied with material on other animal groups; it was established that amphibians, insects and apparently mammals as well as birds are subject to the phenomenon of geographical voice variability, and can thus be utilized as models for study. Immense quantities of data have been accumulated over the last years. The following works are of special interest: W. F. Blair, 1955, 1956, 1958; H. Allard, 1957; B. Alexander and Borror, 1956; A. Faber, 1953; G. Pierce, 1948; H. Frings, 1956. The above authors have collected extensive material on different species of insects and amphibians. No less important is the contribution of ornithologists: Marler, 1956; Thorpe, 1961; Sauer, 1955; Benson, 1948; and others.

An innovation which considerably broadened the scope of bioacoustics was the recent attempt to conduct a parallel study of the voice and hearing mechanisms as a single functional system. Reviews on this subject by J. Schwartzkopff, 1962, and by G. Tembrock, 1959 - which examine the factual material precisely from this point of view - have opened new and unexpected vistas.

Among these is the recently outlined division of geographical voice variability into two basic categories: adaptive variability and nonadaptive variability. Adaptive variability embraces those cases in which the voice serves to indicate the setting apart of individuals or a group of individuals and thus the territory they occupy. This is biologically significant in that it allows animals to utilize the possibilities offered by their ecological niche and thus enables the species to flourish.

At the root of this phenomenon is the well-known individual variability of the voice, which is particularly well defined in birds. A highly developed faculty for sound analysis and excellent coordination of the complex vocal musculature combined with the perfect functioning of higher nervous activity are the most important acquisitions of this group. The physiological mechanism of the highly individual voice variability in birds also enables them to learn at an early age and to imitate the sound elements of their environment. Thus, the individual variability of the voice of a chaffinch indicates, on one hand, the delimitation of its territory, and, on the other, facilitates recognition between mates (Marler, 1956; Thorpe, 1961). In this case the information communicated is primarily intended for one's "own" mate and only to a lesser extent for another's. The individual variability of the voices of penguins and other bird species serve a similar purpose (Borror, 1959; Benson, 1948; Thieckle, 1961; Tembrock, 1959; and others).

Experiments in raising birds under conditions of sound isolation (Kaspar-Hauser isolation chamber), have shown that it is not so much the song that is inherited as a certain rhythm, or way of rendition. In ontogenesis the young bird creates its song with relation to the sound background of its environment, which differs with each individual and group of individual populating different territories. This mechanism of song formation permits the delimitation of a territory, and subsequently facilitates the recognition of a mate (Marler, 1956; Thorpe, 1961). The acquired components influence the calls to a lesser degree, but even they are influenced by differences in geography. This somewhat simplified description becomes far more complicated when one turns to experimental conditions that are as similar as possible to natural conditions. This is demonstrated by the ecological investigations of A. N. Promptov and E. V. Lukina (1945). The majority of species apparently inherit the basic ability to render a song, including the general specific character, the tempo, and sometimes even the pitch. All the other attributes and qualities are acquired (Promptov, 1944).

The establishment of a particular melody in a certain territory is abetted by the fact that the development of the young male's song is completed in the first spring of his life - that is, after his arrival in the district, to which he will return all the following years of his life by force of nesting conservatism. It has been observed that the song of the chaffinch acquires its specific traits as early as autumn; but it becomes more refined and finally stable in the first breeding season (Thorpe, 1961; Marler, 1956). This development of the song in spring lasts several weeks and undergoes no subsequent essential change. Due to this prolonged development of the song, the voice of every individual acquires the characteristics of the group in whose territory the young bird has established residence. Its voice becomes more "comprehensible" to surrounding pairs, even if the bird arrived as a "stranger," genetically unrelated to the group living in the territory.

In the creation of optimal territorial relations within a population, the most important role falls to the song, which is the most adaptable, changeable, and individually variable aspect of the voice (Mal'chevskii, 1958; 1959; Kistyakovskii, 1958; Smogorzhevskii, 1950). These characteristics of the song, together with its identificational functions, are at the same time an essential specific adaptation that indicates, on one hand, the delimitation of the nest territory, and, on the other, serves to attract the female and thus assumes a role in sexual selection.

The delineation of territory is of the greatest importance in groups with pronounced nesting conservatism. In this case the need arises for a permanent "fixation" [the staking of a claim], which signifies the occupation of the territory by the group. This is achieved by certain modes of behavior, and in the event of extremely well-developed hearing and voice mechanisms, sound becomes the most important means for supporting and maintaining the territorial structure of a species. Birds, which are not provided with a well-developed sense of smell, nor with glands that excrete odiferous substances, as in the case of insects and mammals, have vocal-communication systems developed to absolute perfection. The importance of sounds serving as signals increases with the distribution of the species in "closed," easily overlooked biotopes, where sound becomes practically the only certain means of communication and maintenance of contact. Sound orientation acquires an even greater importance under conditions of high population density; or, conversely, when the population is dispersed.

The role of the voice as a means of identification is particularly important in the case of birds with antiphonal song (Cisticola, Trachyphonus, Laniarius) that live in dense thickets, where the role of visual signals is reduced to a minimum. All the principal behavior patterns (recognition of the mate, nuptial display, patrol of the territory, etc.) are achieved here almost exclusively by means of the voice. Each pair of birds living under the above conditions has its own song pattern (Thorpe, 1963).

Similar conditions bring about the intensification of vocal-communication in both sexes in other orders. For instance, in owls the necessity for vocal communication is apparently caused not only by the limited visibility under conditions of "closed biotopes" but is also related to their nocturnal way of life (Kistyakovskii, 1958). In the cuckoo the same phenomenon is due to its polygamous way of life. Sometimes it is not the male but the female who clearly establishes her individuality by making a loud call, which causes her to stand out against the background of surrounding sounds. The male then seeks her out by her voice (as described for painted snipes, button-quails, phalaropes, and some species of Anatidae, by Kistyakovskii, 1958).

By mastering and using the signals of other species, some of them even belonging to different classes, species which specialize in the imitation of the elements of their sound environment elaborate the

isolating mechanisms of individual pairs and their groups. Yet they provide the biogenic sound background of the biotope, landscape, etc., with a highly specific character. It is well known that many wheat-ears incorporate the screams of gerbils, susliks and many other species into their song pattern (Varshavskii, 1959). Warblers and mockingbirds often imitate the voices of birds of prey. Consequently, the acquired, the "learned" component can be utilized and already is utilized as a finely differentiated zoogeographical criterion.

In a number of cases the "learned" component in mockingbirds may even be inherited, especially in those cases where too great a proportion of foreign sounds in the song begins to interfere with communication. Thus, according to A.B. Kistyakovskii (1958), the crackling musical phrases of the warbler have apparently become inherited by the red-spotted bluethroat, and the whistling of the redshank (Tringa totanus) by the skylark.

Group (population) variability of the voice, manifested in the above-mentioned local dialects, was described as early as the 18th century by Thomas Ward, and was re-discovered by Lucanus in 1907. The smallest groups recognizable by their local dialects sometimes occupy territories of not more than a few hectares, and sometimes even less. Described with the example of several species, especially of the Isabelline Wheatear and of the red-headed bunting (by S.N. Varshavskii, 1959) and of the thrush (by A.S. Mal'chevskii, 1959), they are apparently groups of closely related families of different taxonomic rank. It is quite possible that some of them cannot be compared in size with the basic population. Others, on the other hand, may correspond to the basic and ecological populations. The local dialects of these small groups are not stable. They have their own dynamics, they disappear and re-appear, change with the territory, etc. In other words, they are not yet fixed genetically, and are phenotypical phenomena.

More stable are the dialects of large territorial groupings; according to our own terminology - geographical populations. These "vocal races" have been discovered within the limits of one subspecies, and are not characterized by any systems. An excellent study was made by F. Marler and M. Tamura (1962) on the voices of geographical populations of Zonotrichia leucophrys, the white-crowned sparrow. The first investigations of geographical differences of the chaffinch were made by N.I. Dergunov (1925). Subsequently they were considerably enlarged and supplemented by A.N. Promptov (1930), in a book which became a classic, authoritative work. Geographical differences have already been established in the singing of chaffinches in the surroundings of Moscow, in the Southern Urals, in the Alps, the Mediterranean regions and Greece (Promptov, 1930; Marler, 1956; Stresemann, 1942; Sick, 1939; Steinbacher, 1927). The rain-call of that species is also subject to geographical variability. South German, Alpine and Mediterranean blackcaps do not sing in the same manner (Sauer, 1955; Emeis, 1957). Benson (1948) found geographical variability in the voices of 33 species of passerines in Central Africa. Borror (1961) established

that the Carolina Wrens (*Thryothorus ludovicianus*) in Florida differ in their songs from those of Ohio. The little bunting of Sweden, Norway, Schleswig-Holstein and Denmark sings differently from that of Eastern Europe (Solomonsen, 1935). Geographical voice variability has also been established for the pika, various Fringillidae, tits, night-jars, and many others (Thieckel, 1961; Stadler, 1917, 1930; Thoenen, 1962; Peterson, 1941). Instrumental sounds are also subject to geographical variability, as they actually have the same functions. According to Blum and Young (1958), the drum roll of the black wood-pecker in Holland lasts 3.5 seconds, and in Germany - 1.5 seconds.

Among insects and amphibians, the voice apparently is hardly used at all as a marking signal of small intraspecific groups (Blair, 1955, 1956; Frings, 1958). This is mainly due to their morphologically imperfect vocal apparatus and a lower organization of higher nervous activity. In these groups the voice is apparently mainly used as an isolation mechanism in higher taxonomic divisions (species and subspecies).

Among insects and amphibians there is widespread nonadaptive geographical voice variability, which does not include any "marking" properties but is related to the general influence of climatic and other landscape factors on the metabolism, and, consequently, on the voice as well. In recent years there has appeared much data on the nature of the climatic conditions influencing the voice of insects (Hukusima, 1948; Harz, 1956), amphibians (Blair, 1955, 1958), and even birds (Heyder, 1954; Sick, 1939; Peitzmeier, 1955; Schwan, 1921-22). Under the influence of temperature and humidity there occur changes in the frequency characteristics, intensity, and even qualitative character of individual syllables. But in birds the changes usually affect the rhythm of the singing (Scheer, 1952; Thorpe, 1961). In this case we consider the dependence of the voice on natural conditions a particular feature of the general phenomenon of ecological-geographical isomorphism, the idea of which, in its application to animals, was elaborated by G.P. Dement'ev (1948, 1951).

Geographical voice variability in insects is a subject which has occupied many investigators. A. Faber (1953) was one of the first to establish this phenomenon. H. Jacobs (1957) observed differences in the voices of insects of the locust family in Munich and the Tyrol. Pierce (1948) described the geographical voice variability of Nemobius fasciatus. Highly interesting and informative work on amphibians as carried out by Blair (1955-1962). A good review of the cases mentioned in the literature can be found in the works of Schwartzkopff (1962).

But the geographical variability of voice not only perfects itself in the process of evolution - it also exercises an ever-increasing influence on the processes of form and species formation, acting as an isolation mechanism. In this respect the coincidence of geographical voice variability within species and subspecies is of considerable interest.

Thus three subspecies of quail: the African (Coturnix coturnix africana), the Japanese (C. c. japonicus) and the European (C. c. coturnix) can be easily differentiated by their voices. Parus atricapillus salicarius differs from P. a. rhenanus by its call. Zonotrichia capensis antillarum from San Domingo has a much louder song than other subspecies. According to Pierce (1948), the frequency of the voice of Nemobius fasciatus fasciatus is 7,500 cps, while in Nemobius sociabilis it is 7,740 and in N. f. tintulus 6,300 (1961). A good review of the interspecific variability of birds' songs was written by Borrow (1961).

The processes of sympatric and allopatric species formation, and partial or complete overlapping of distribution areas, are clearly reflected in the voice. These processes produce cases in which the voices in an area in contact with that of a closely related species or subspecies differ more strongly than voices in areas having no contact.

Thus in the group Bufo americanus (Blair, 1962), Bufo woodhousei differs more markedly from the sympatric Bufo terrestris from Louisiana and Georgia than from the allopatric Bufo terrestris from Florida. Bufo woodhousei also differs to a greater extent from the sympatric Bufo americanus from Oklahoma than from the allopatric Bufo americanus from Wisconsin and Michigan.

Microhyla olivacea and Microhyla carolinensis have different voices in contiguous areas; but in more distant parts of their areas have more similar voices (Blair, 1955). Similar cases are described, offering as examples the willow warbler, Palla's warbler, some Hylocichla and others (Tembrock, 1959). Of great interest are the data published by Thoenen (1962). According to his investigations, Parus montanus montanus is easily distinguished from P. m. salicarius in the Alpine zone. But the Alpine P. montanus resembles the American P. atricapillus and P. carolinensis in its song. There is greater resemblance between P. m. salicarius and P. palustris than between P. m. montanus and P. m. salicarius. The differences between the songs of P. m. montanus and P. m. salicarius are so great that the birds do not "understand" each other at times.

All the above-mentioned demonstrate, without a doubt, that sound mechanisms play an extremely important role in the processes of intra-specific (populational) and specific divergence, especially in the case of birds. It has become clear that at present we underestimate the importance of this role. Further development of investigations in this direction will undoubtedly produce valuable new data concerning the mechanisms of populational and specific isolation, and will serve to broaden our concepts of the mechanisms of microevolution.

Local dialects, while reflecting and preserving the complex and involved patterns of the specific population, also acquire traits of complexity and of heterogeneity. Some investigators (Thorpe, 1961; Marler, 1956) make use of this fact in order to deny the functional importance of local dialects. Marler (1956), for example, considers them by-products of the imitative faculty of birds, and relates

population variability exclusively to the genetically fixed song. This tendency is also clearly noticeable in the work of Marler and Tamura (1962) on the voice of Zonotrichia leucophrys. In our opinion, the absence of uniformity in the local dialects of various species and groupings is an additional argument in favor of the further development of hierarchical classification of dialects, and their comparison with the classifications of populations existing in ecology. The need for further study is already definitely felt.

Of special interest is the system worked out by N.P. Naumov, according to which genetically isolated populations regularly merge into a single system with phenotypical populations. The attempt to apply the same principles to the classification of vocal dialects appears justified to us, especially since with birds, as we have attempted to explain, the voice happens to be the most flexible and convenient mechanism for fixation (marking) of any grouping, beginning with single specimens and pairs (as is the case with antiphonal species), and up to several groups of families and populations.

The principles and methods of coding geographic information in the voice of animals present a somewhat separate problem. Valuable material has accumulated on this subject in recent years. It happens that geographical variability of the voice has a close, though rather peculiar, relation to the apparatus of sound analysis. This circumstance has become especially important after the discovery of the so-called "secondary" or "accessory" sounds in the voice of animals: sounds which, according to some authors, have no functional significance. These sounds arise together with the rendering of the basic, biologically important ones. Thus, in the voice of birds there are ultrasonic frequencies reaching 45,000 cps, while it is currently believed that the upper limit of their sound registration is only 29,000 cps (Schwartzkopff, 1962). W. Thorpe and D. Griffin (1962), who made a special investigation of this problem, have found ultra-sounds in the voice of Locustella naevia, Erithacus rubecula, Emberiza calandra, Sylvia communis, Acrocephalus scirpaceus, and others. Inasmuch as naturally registered sounds have a functional significance, it is tempting to connect the nonadaptive geographical variability of voice with secondary sounds. However, this assumption requires further investigation and development. Besides, the possibility is not excluded that many of those sounds which until now have been considered as secondary may in reality have a functional significance.

The importance of the sound analyzer* as a system limiting any functional reorganization in the voice is first of all expressed in the extreme differences in acoustic means utilized for the transmission of information by groups having different levels of hearing.

* [According to Pavlov, an analyzer consists of the nerve endings, peripheral nerves and cerebral connection of one particular faculty; there are thus auditory, olfactory, gustatory, cutaneous and motor.]

Thus geographical variability in the voice of insects and amphibians is based on sharp fluctuations of both frequency and intensity. Nemobius fasciatus achieves the transmission of relevant information by frequency variations in a spectrum of 200 to 1,000 cps (Pierce, 1948). Sometimes the number of syllables (Jacob, 1957) or temporary peculiarities of each syllable (Faber, 1953; Allard, 1957) indicates special meanings. In the voice of amphibians frequency variations play an important role (Blair, 1955-58). Geographical information in the voice of birds can be coded according to the same principles, though more often than not it is coded by finer variations in the singing.

Thus, the races of Parus atricapillus are distinguished by their loud call, those of Zonotrichia capensis by the rapidity of their rendition of certain elements of their song, and those of Emberiza or Coturnix by the presence or absence of an introduction (Salomonsen, 1935; Chapman, 1940; Borror, 1956).

Quite often information is conveyed not by a special song but by a particular aspect of its rendition. Thus Finnish and English nightjars (Caprimulgus) sing at different times of day and night (Tembrock, 1959).

The high level of development of the analyzer and of the higher nervous activity in birds produces the following phenomenon: geographical voice variability in birds is as a rule related to the separate parts of the spectrum. On the other hand the stridulation of insects and the rather monotonous voices of amphibians vary throughout their entire spectrum. All this has a definite biological significance.

The functions of insect and amphibian voices, as compared to the voices of birds, are considerably more restricted. In birds the voice plays a part in all the principal phases of life: pairing, migration, rearing of the young, defense against predators, etc., which explains the rich range of possibilities in birds' voices. Cariama cristata alone possesses over 200 notes; Passeriformes, of course, have many more notes at their disposal. Yet, although each of these notes can be utilized for conveying several different signals, the possibilities of coding them in that direction are not infinite. (A single note produced by passerines can have up to 15 connotations, depending on its variations.)

In certain cases there arises the need for preserving the stability of the "meaning" of a signal and of restricting its functional load. In other cases the opposite is true, and a greater polyfunctionality is required.

Thus, for example, single phrases in the song of the chaffinch may serve many purposes: delimitation of territory, identification of a mate or a pair, danger signals, mating calls, nuptial display, flocking signals and so on. (Marler, 1956). The element of geographical variability has very little effect on these functions, but can also be

included in these phrases. On the other hand the screams of the young birds (nestlings), which indicate only one thing - hunger - are narrowly specialized, stable, and do not carry any additional connotations, such as geographical information. Besides, there is no biological justification for the latter. Thus, the coincidence of geographical (population) variability with certain elements in the voice of birds has an adaptive character and is the result of an important evolutionary acquisition - the narrow specialization of separate elements.

Until recently the problems of the acoustics of associations did not arouse any particular interest. In our opinion they are of considerable interest, since each of the mechanisms of vocal communication is formed not only under the influence of one's own species and physical environmental conditions but is also influenced by the general biogenous sound background, which is characteristic of the habitat in which the species evolves.

The physical foundations of the acoustics of natural zones and landscapes have also been insufficiently investigated, and our information is scant. The greatest differences are noticeable in the case of "closed" and "open" habitats. Thus, for instance, in the tundra the distance a voice carries is limited by air humidity, but the weak absorption of sound by the extremely humid soil is a compensatory factor. In the forest the distance a voice carries is greatly reduced owing to the strong absorption and multiple reverberation of sound by tree trunks, branches and leaves. In steppes the development of the grass cover creates the conditions of a "closed" landscape for many animals. In the desert, the sound-absorbing properties of sandy soils are unfavorable to the propagation of sound. Another phenomenon with a similar effect is the particularly active air movement produced by constant winds, convection of heated layers, etc. Similar conditions influencing the propagation of sound also exist in the various biotopes.

It is therefore natural that such marked differences in conditions exert a considerable influence on the mechanisms of vocal communication. Species which have become adapted to life in open spaces tend toward a generally limited reliance on sound signals, and utilize visual cues to a greater extent. This can be easily observed in Ratitae, Otididae, Cicoriformes, sandpipers, cranes, etc.

Observations have shown that the nature of vocal communication may serve as an indication of the place of origin, development and further expansion of a group. It can also indicate the antiquity of its' link with a particular landscape and type of association.

The influence of the biogenous background on sound signalization is also subject to the laws of geographical variation. It is closely related to the structure and stratigraphy of associations. The following changes in the role of the biogenous background in the formation of sound signalization can be observed from north to south, from the tundras towards zones of optimal life conditions.

Under tundra conditions the degree of sound saturation of the environment is rather limited, and its formative influence therefore insignificant. The ability to see great distances in the surroundings, together with a weakly developed sound background, results in a simple song pattern in autochthonous tundra birds. With other morphological indices as well, differentiation between single individuals and pairs depends on the distance at which communication can be continuously maintained by vocal contact.

Proceeding southward one finds that, together with the increasing complexity of the environment, the structure and stratigraphy of associations also become more complicated. Interspecific relations acquire greater importance, as does, in particular, the natural sound background, which plays an increased role in the formation of mechanisms of vocal contact. The biogenous sound background reaches its highest degree of saturation in the so-called "bird markets," i.e., in mixed forests consisting of coniferous and broadleaved trees, and in broadleaved and tropical forests. When speaking of associations inhabiting these types of forests, it is possible to speak of the objective existence of an involved acoustic structure. There arises here a definite need for the strictest form of animal adaptation, since sound signals have to be easily recognized and differentiated by their frequency, intensity, pitch, modulation and general pattern, over and above the general choral background. Should this fail to be achieved, the birds are in danger of having their means of orientation and communication greatly reduced. The problem is to find a "free area" in the acoustic field, that is, one not filled with signals of the same parameters. In addition, the importance of other means of orientation in the forest, such as visual perception, becomes greatly reduced. With a weakly developed sense of smell, sound communication becomes the only really certain means for maintenance of contacts. All this makes it difficult to find such a "free area," which we suggest calling an "acoustic niche."

Data obtained from recording and analyzing voices already indicate the existence of such niches. The peculiarities of sound signalization in the Turdidae family are sufficient to give an idea of how originally and rationally vocal communications are organized among these birds.

In our opinion, comparisons of the biogenous sound backgrounds of various faunistic complexes of high taxonomic rank are of special interest. They will undoubtedly show correlations and parallelisms of which we as yet have only the vaguest idea. Investigations in that direction will be of great help not only for discovering the laws of formation and evolution of the mechanisms of vocal communications, but also will perhaps help in defining certain aspects of the general character of evolution with greater precision.

However, data on the bioacoustics of associations have not only an exclusively scientific interest. During recent years their great practical importance has been demonstrated. This is clearly illustrated by the practical application of such knowledge to associations in oceans

and seas, where the study of the biogenous sound background has opened new practical vistas for perfecting methods of underwater navigation. Such investigations, carried out in France and other countries, have led to the idea of drawing up "acoustic underwater sea maps."

Thus, one can see that the present successes of the science of bioacoustics, especially in its geographical aspects, have found increasing application in related biological fields, touching, as it does, upon many major problems, among which one can primarily number bionics, the laws governing animal behavior, ecology, geography, the evolution of populations and associations, and, in addition, problems concerning the formation of forms and species, structure, formation and dynamics of fauna, etc. Further development in the study of bioacoustics promises data of the greatest interest in all the above fields.

BIBLIOGRAPHY

Publications in Russian

1. Dement'ev, G.P. Issledovaniya po okraske pozvonochnykh zhivotnykh, 3. Pravilo klimaticheskikh variatsii okraski ptits i mlekopitayushchikh (Investigations on the Coloring of Vertebrates, 3. Laws of Climatic Variations in the Coloring of Birds and Mammals.). - Zoologicheskii Zhurnal, 37(1):47-52. 1951.
Sokola - Krechety (Falcons). - Izdanie Moskovskogo Obshchestva Ispytatelei Prirody. Moskva. 1948.
2. Dement'ev, G.P. and V.D. Il'ichev. Golos ptits i nekotorye voprosy ego izucheniya (The Voice of Birds and Some Problems in its Investigation). - Ornitologiya, No. 6: 401-407. 1951.
3. Dergunov, I.I. Biologicheskie zametki (Biological Notes). - Listki Biologii. Stat'i Yunykh Naturalistov, No. 15: 19. 1925.
4. Kistyakovskii, A.B. Polovoi otbor i vidovye opoznavatel'nye priznaki (Sexual Selection and Signs of Specific Recognition). - Izdanie Kievskogo Universita. Kiev. 1958.
5. Mal'chevskii, A.S. Mestnye naevy i geograficheskaya izmenchivost' pesni u ptits (Local Melodies and Geographical Variability of Birds' Songs). - Vestnik Leningradskogo Universiteta, No. 9: 110-119. 1959.
Gnezdovaya zhizn' pevchikh ptits (The Nesting Life of Song Birds). - Izdanie Leningradskogo Universiteta. 1963.

Ob izuchenii golosov ptits (The Study of Birds' Voices). - Trudy Leningradskogo Obshchestva Estestvoispytatelei, 74(1): 57-61.

6. Promptov, A.N. Aberratsii i izmenchivost' pesni ptits kak kriterii v izuchenii postoyanstva obitanii populyatsii (Aberrations and Variability in Birds' Songs as a Criterion for the Study of Permanency of Habitats of Populations). - Uragus, No. 2. Tomsk, 1930.
Geograficheskaya izmenchivost' pesni zyablika (*Fringilla coelebs* L.) v svayzi s obshchimi problemami sezonnnykh pereletov ptits (Variability of the Song of Chaffinch (*Fringilla coelebs* L.) in Connection with General Seasonal Problems of Bird Migrations). - Zoologicheskii Zhurnal, 10(3):17-40. 1944.
Golosavaya imitatsiya ptits kak odno iz spetsificheskikh svoistv ikh nervnoi deyatel'nosti (Voice Imitation in Birds as One of the Specific Properties of their Nervous Activity). - Doklady Akademii Nauk SSSR, 45(6):278-281. 1956.
Ocherki po probleme biologicheskoi adaptatsii povedeniya vorib'inykh ptits (On the Problem of Biological Adaptation of the Behavior of Passerine Birds). - Moskva-Leningrad.
7. Promptov, A.N. and E.V. Lukina. Uslovno-reflektornaya differentsirovka pozyvov u vorob'inykh ptits i ee bioilogicheskoe znachenie (Conditioned-Reflex Differentiation of Calls in Passerines and its Biological Significance). - Doklady Adademii Nauk SSSR, 16(9):422-424. 1945.
8. Simkin, G.N. and V.D. Ill'ichev. O geograficheskikh aspektakh bioakustiki (On the Geographical Aspects of Bioacoustics). Zoogeografiya sushi (Land Zoogeography). Synopses and Reports. - Tret'e Vsesoyuznoe soveshchanie po zoogeografii sushi. Tashkent. 1963.
9. Smogorzhevskii, A.A. K voprosu o znachenii peniya i gnezdovoi territorii u ptits (On the Problem of the Importance of Song and of Nesting Territory for Birds). - Trudy Zoologicheskogo Mizeya Kievskogo Universiteta, No. 11:103-107. 1950.
- 9a. Varshavskii, S.N. O geograficheskoe izmenchivosti pesni kamenki-plyasur'i i zhelchonci ovsyaniki v svyazi s gnezdovym konservatizmom u ptits (Geographical Variability of the Song of the Isabelline Wheatear and Red-Headed Bunting in Relation to Nesting Conservatism in Birds). - Tezisy Dikladov, 2 - oi Vsesoyuznoi Ornitologicheskoi Konferentsii. Moskva. 1959.

[For remainder of bibliography, in non-Russian languages, see original paper - JAP].