ZAKŁAD ZOOLOGII SYSTEMATYCZNEJ
POLSKIEJ AKADEMII NAUK

ACTA ZOOLOGICA CRACOVIENSIA

Tom XIV Kraków, 31. XII. 1969 Nr 16

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Migratory and stationary bats (*Chiroptera*) of the European part of the Soviet Union

[Pp. 393—440 and 4 figs.]

Wędrowne i osiadłe nietoperze (*Chiroptera*) europejskiej części Związku Radzieckiego

Перелетные и оседлые виды летучих мышей (*Chiroptera*) в европейской части СССР

Abstract. All materials available to the author and concerning the hibernation and migrations of bats in the European part of the U.S.S.R. were used as the basis for the present study. The bat species occurring in this region may be divided into two groups: the group of stationary bats and that of migratory ones. The first group includes bats *(Rhinolophus, Myotis, Barbastella, Plecotus* and *Eptesicus)* found in more than 90 natural and artificial caves in winter. Its subgroup of Boreal species living in the severe climate of Central and Northern Russia was analysed most closely. It is supposed that the winter shelters of these bats embrace not only caves and that the bulk of the population winters in other hiding places, unknown as yet. Six migratory species *(Nyctalus, Pipistrellus, Vespertilio)* leave the central and northern regions of the European part of the U.S.S.R. for their winter quarters in Central and South-Eastern Europe. The data on the phenology of migration based on visual observations and results of banding were also analysed; 39 long flights, covering 350—1600 km. were noted. In summer a strong quantitative predominance of females and even complete lack of males were observed in most of the migratory species. The causes of long migrations of bats in Eastern Europe, the relation of the geographical ranges of hibernation to the climate, and the biological differences, connected with the adaptation to shelters of various types, between the stationary and migratory species were considered.

CONTENTS

I. INTRODUCTION

It was completely obscure until quite lately where and how the bats of the vast territory of the European region of the U.S.S.R. spend winter. It was known only that they disappear in the period from autumn till spring and, as hardly any specimens were found hibernating, the general view was that, like migratory birds, most bats leave their summer quarters in the autumn and hibernate away from them. It was even supposed that some species fly away to the Tropics, where they remain active throughout the winter and have a second brood. In his monograph of the bats of the U.S.S.R. KUZYAKIN (1950) stated that for the huge majority of bats the place of their winter stay was unknown.

The situation has changed in the last 10 years. A weighty contribution to the knowledge of the biology of bats was the book on the bats of the Ukraine by ABELENTSEV et al. (1956), in which the authors sum up their observations of many years. It contains a great many new data concerning the winter quarters and seasonal migrations of bats and their division into stationary and migratory species, offered and substantiated by the authors. However, their investigation was confined to only one region and did not constitute a basis for far-reaching generalizations, whereas the enormous territory of Central and Northern Russia was still a „blank space" as regards the knowledge of the wintering sites of bats. In order to fill this gap I carried out field investigations in the Ural Mts., in Povol'zhe and in the central and northwestern regions of the European part of the Soviet Union in 1952—1957 and collected the whole literature of the subject (STRELKOV, 1958). I have been complementing the materials concerning the wintering of bats in different regions of the U.S.S.R. ever since. Remarkably more is also known of the long migrations of bats owing to the data acquired recently by mass banding (KAMENEVA and PANYUTIN, 1960, 1964; KURSKOV, 1965; POKROVSKII and SHCHADILOV, 1962; PANYUTIN, 1968).

The accumulation of new materials in the Soviet Union and abroad necessitates their analysis and subsequent formation of general conclusions. This is the task I have taken up in the present study in the hope that it will prove useful for future investigations of bat biology.

I particularly wish to express my thanks to V. I. ABELENTSEV and K. K. PANYUTIN, who allowed me to use their unpublished observations, and to

Dr G. NATUSCHKE (German Democratic Republic) for his valuable information and bibliographical data.

I am very grateful to Mr. J. Zawadzki for his translation and to Dr. A. Krzanowski for editing my paper.

II. STATIONARY BAT SPECIES

In the European part of the Soviet Union wintering bats were found almost exclusively in caves or other similar artificial lodgings: abandoned shafts, underground galleries, quarries, etc. Since the ecological conditions provided by them, such as their constant and moderately low temperature, high relative humidity, and darkness, are more or less the same, in the further parts

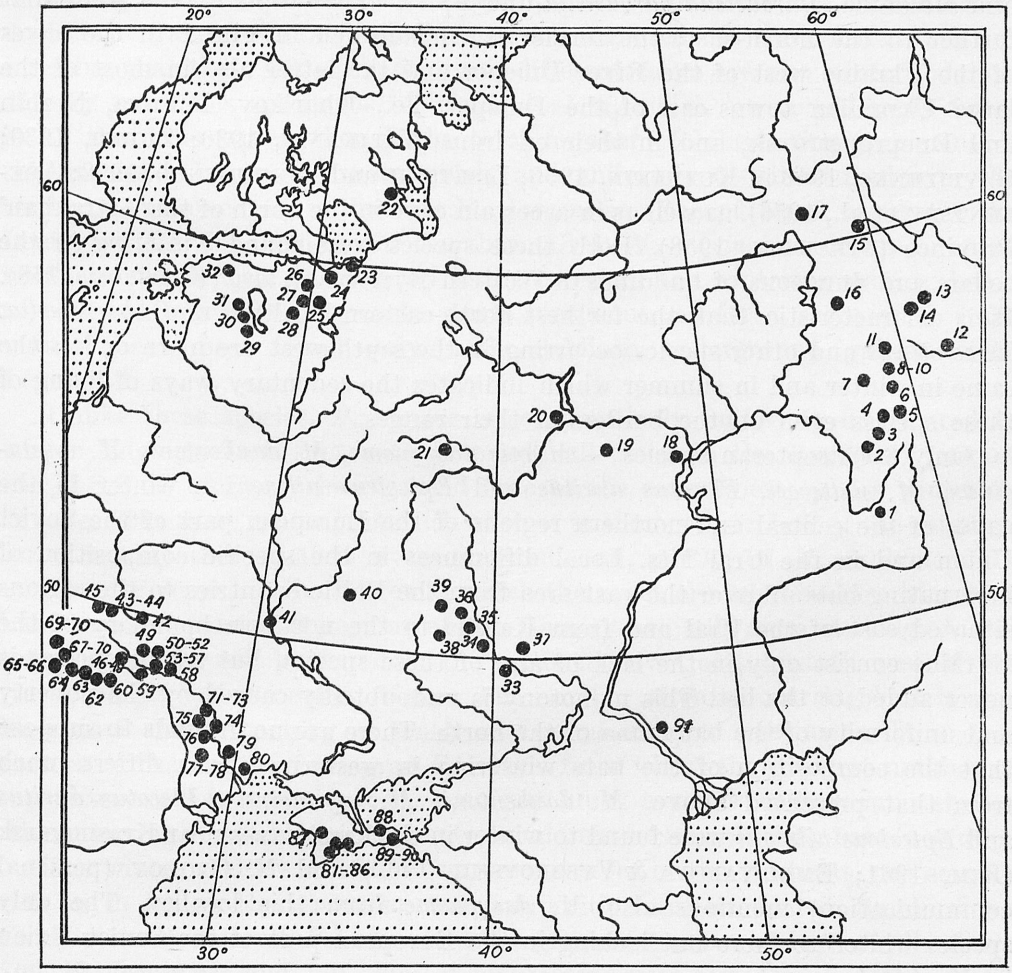

Fig. 1. Localities in which bats hibernate in caves in the European part of the U.S.S.R. The names of caves, their numeration and the specific composition of the bats wintering in them are given in Table I

of this paper I shall refer to all such underground shelters as caves. So far I know above 90 caves or groups of caves in which bats take shelter in winter (Fig. 1). On the basis of these data it is possible to give the specific composition of the there wintering bats as well as the ecological conditions of wintering.

Out of the 24 bat species found in the European part of the Soviet Union (excluding the Caucasus), 16 were found in caves, which forms about 70 per cent. As will be seen from Table I, the caves of the southern and south-western part of the country have the quantitatively and qualitatively richest bat fauna. As we move northward, the specific composition of the wintering bats impoverishes considerably. Thermophilous species, pertinent to South and, partly, Central Europe (*Miniopterus*, *Rhinolophus*, a number of species of *Myotis*, and others) are confined to the Crimea, Transcarpathia, Subcarpathian Ukraine, and Moldavia. *Barbastella barbastella* and *Eptesicus serotinus* extend somewhat farther to the north-east; the former is encountered in winter in the caves of the Ukraine west of the River Dnieper and the latter also in most of the large Ukrainian towns east of the Dnieper, i.e., Khar'kov, Poltava, Nezhin and Dnepropetrovsk, and in their environs (Velikaniv, 1930; Zubko, 1939; Gavrilenko, 1948 in Kuzyakin, 1950; Lisetskii and Kunichenko, 1952; Abelentsev et al., 1956), as well as in a certain cave in the north of the Astrakhan' Province (Strelkov, 1958). Both these species were found wintering in the cellars and dungeons of buildings in Western Byelorussia also (Kurskov, 1958). It is characteristic that the farthest north-eastern localities of *B. barbastella*, *E. serotinus* and other species occurring in the south-west are more or less the same in winter and in summer which indicates the sedentary ways of living of these species even on the borders of their ranges.

Only 6 Chiropteran species — *Myotis dasycneme*, *M. daubentoni*, *M. mystacinus*, *M. nattereri*, *Plecotus auritus* and *Eptesicus nilssoni* — winter in the caves of the central and northern regions of the European part of the Soviet Union and in the Ural Mts. Local differences in the specific composition of hibernating bats all over the vast area from the Baltic countries to the regions situated east of the Ural and from Karelia to the northern boundary of the Ukraine consist only in the lack of any of these species, but a new species is never added to the list. This monotony is undoubtedly caused by the poverty and uniformity of the bat fauna of the north. There are no grounds to suppose that the composition of the bats wintering in western Siberia differs much from that presented above. *M. daubentoni*, *M. mystacinus*, *Plecotus auritus* and *Eptesicus nilssoni* were found to winter in the karst caves near Krasnoyarsk (Kim, 1961; Emel'yanova & Vysokovskii, 1962) and N. Ovodov (personal communication) mentions also *M. dasycneme* from this locality. The only species wintering there but lacking in the European part of the Soviet Union is *Murina leucogaster*.

I shall consider the group of Boreal species more closely below, because the possibility of their wintering under severe conditions of the central and northern regions of the Soviet Union has not been examined sufficiently well

and the opinions can be found in literature that they go on long seasonal migrations. Beyond the frontiers of the Soviet Union these species are well known for their wintering in caves in Central and North Europe.

I have already published (STRELKOV, 1958) a detailed survey of most of the known localities of wintering bats in Central and Northern Russia. In spite of all the monotony in the composition of the hibernating bats, attention is drawn by their huge quantitative and qualitative diversity, as regards particular shelters (Table I). This phenomenon is certainly connected with the unknown properties of the distribution of bats, especially with their rare occurrence, which in many species is observed also in summer. For example, *M. dasycneme* hibernates in only 12 caves in the European part of the U.S.S.R.; 10 of these caves have small numbers of wintering specimens, whereas in the remaining 2 caves (Smolinskaya Cave in the Middle Ural Mts. and Staroladozhskaya Cave near Leningrad) there are hundreds of these bats. It is interesting that these two ecologically so different caves are also winter lodgings of very numerous specimens of *M. daubentoni*, which are considerably fewer in all the other caves, though the total number of hibernating specimens of this species is larger and more widely and uniformly distributed all over the territory examined than that of *M. dasycneme*. Except for 2 caves (in the Leningrad Province and in the Northern Ural) *M. mystacinus* occurs in small numbers everywhere. *M. nattereri* is the rarest of the wintering species, being represented everywhere by only single specimens; so far a score or so individuals have been found only in the Sablinsk underground galleries near Leningrad.

Unlike these species, *P. auritus* is comparatively uniformly distributed in winter lodgings. It is met with in nearly all caves in the European part of the U.S.S.R. and may be regarded here as the commonest species wintering in caves. The same is also true of *E. nilssoni* in the northern half of the country, for it is only there that it is encountered, and, partly, of *M. daubentoni*.

The differences in the degree in which the caves are inhabited by wintering bats between particular regions of the country are still more striking. A full set of 6 species will be found in the artificial caves of the north-west of the European part of the Soviet Union. The number of bats occurring here is also high, in 2 caves reaching as many as several hundred specimens. It is characteristic that in the Leningrad Province, from where the greatest number of my observations were obtained, I do not know a single underground shelter which, having a suitable microclimate, would not be inhabited by bats in winter.

The winter shelters of bats in numerous caves of the Ural Mts. are equally rich in so far as their number and composition are concerned. Smolinskaya Cave in the Sverdlovsk Province had the greatest number of bats of all: above 700 *M. dasycneme* and 150—200 *M. daubentoni* were found in it in the winter of 1956.

There are very few bats in all the artificial caves of the Central Chernozem Provinces of the European part of the U.S.S.R. Suffice it to say that in all

the 9 caves examined by me I counted hardly 61 hibernating bats altogether, none of these caves having more than 15 specimens. The number of species represented was also extremely small. However, according to the information received from the local people, large colonies of bats of several species hibernated in Galievskaya Cave in the Voronezh Province and in the stonepit on the River Oskol in the Kursk Province before the Second World War, whereas in small karst caves near Lipetsk (BARABASH-NIKIFOROV, 1957) hikers are said to have observed up to 100 wintering bats not long ago. It would be very instructive to have this information checked.

For a long time no wintering bats at all could be found in Middle Povolzh'e. I failed to find them in any of the 7 caves and underground galleries examined in the Tatar A.S.S.R., though, as regards their microclimate, they are quite fit for winter shelter. V. A. POPOV (1960), too, has practically no data on the wintering of bats in this region, although he collected materials concerning the mammalian fauna of Middle Povolzh'e for a score years or so. It was not until quite recently that some Moscow speleologists have found wintering bats in 2 karst caves in the Gor'kii Province.

The causes of these differences are obscure. It is possible that they result from various degrees of exploration of the caves in different parts of the country; the more so, since these shelters differ considerably from each other in size, origin, and degree in which they are frequented by people, from locality to locality. It may well be that particular populations of bats differ in their habits: in some parts of the country they may winter in caves, in others avoid them.

In spite of the differences presented above I consider all the Chiropteran species listed as wintering in caves to be relatively sedentary, i.e., remaining in winter in the central and northern regions of the European part of the Soviet Union. This conclusion is confirmed not only by the fact that they have been found repeatedly in their winter lodgings, among other places, at the northern boundaries of their distribution, but also by indirect evidences. No seasonal mass passages of the species wintering in caves were observed in the southern and western regions of the country, though the Ukrainian zoologists carried out special studies of bat migrations (ZUBKO, 1937; POPOV, 1941; ABELENTSEV et al., 1956). The data offered by Lavrov (1953), who watched regular spring migrations of all bat species, including *M. dasycneme* and *M. mystacinus*, in the Voronezh Reserve are very interesting, but his observations are not very precise and they still fail to prove that these migrations were long ones.

Neither in summer nor in winter are the Boreal species met with in the southern areas of the European part of the U.S.S.R., or at the most they occur there in very small numbers. In the West, i.e., in Central Europe no mass migrations from the north-east were recorded and the banding of bats in caves in the winter provided no bases to conclude that the there living bats make long migrations. Finally, neither does the existence of morphological differences, however small they are, between the populations of *M. daubentoni*,

M. dasycneme and especially *M. mystacinus* of East Europe and those of the western Ukraine, Byelorussia and — as regards *M. mystacinus* — also of the Crimea, southern Ukraine and Caucasus (OGNEV, 1928; ABELENTSEV et al., 1956) corroborate the occurrence of long seasonal migrations of these species. For in the northern species copulation falls to a great extent in winter (STRELKOV, 1962) and, consequently, the close contact of various populations in common winter shelters would not have allowed the geographical intraspecific morphological differentiation.

Unfortunately, our knowledge of the manner and places of wintering of the sedentary species is still unsatisfactory, especially because it is confined nearly exclusively to the finds of bats hibernating in caves, which are regarded as a sort of indicators of the wintering bats in the given region. However, caves are rare in a great part of the European territory of the Soviet Union, and in large areas they are lacking at all. The overwhelming majority of the shelters examined are man-made „caves", but in most areas even these are absent. Besides, all the artificial „caves" were formed a relatively short time ago, and for this reason they could not be original winter shelters of these mammals.

It is also very characteristic that most of the caves examined were inhabited by considerably fewer bats than might have been expected, seeing how scarce the shelters of this type are.

I was unable to make any detailed quantitative calculations, but the small number of caves and that of bats in most of the caves indicate decidedly that in the European part of the U.S.S.R. caves are sites of wintering of only a small part of the population living in these areas in summer. This leads to the supposition that the bats winter not only in caves; a remarkable part of the population spend winter in some other, so far unknown, hiding places. Moreover, it may be assumed that they managed to colonize the vast plains of East Europe just owing to their relative independence on caves. The distribution of a number of other species, biologically more specialized and both in summer and in winter closely associated with caves, is chiefly restricted to the mountainous ridges of the Carpathians and mountainous areas of the Crimea and Caucasus, abounding in caves. The large regions stretching in the north and east have no caves, which fact together with the change in climate and landscape stop the further spread of these species.

Unluckily, we have hardly any reliable information about the wintering of bats out of caves, which is partly explained by the inaccessibility of such shelters, small numbers of bats in the north, difficulties of search, and plainly by the fact that such field studies have scarcely been carried out at all.

Out of caves the bats do not gather in large numbers but winter scattered, singly or in small groups. Such specimens are oftenest found quite incidentally in various parts of dwelling houses and farm buildings: near chimneys in attics, in disused chimneys, behind the board lining of wooden walls, in vaults and cellars, in boarded wells, ruines, haystacks, etc. It should be emphasized that

in the severe climate of Russia these hiding places are often unsufficiently insulated from the outer environment and they get very cold during spells of frost; bats happened to be found wintering in such lodgings at as low a temperature as −5° C.

In rare instants when I managed to lay my hands on such specimens and determine the species, they usually appeared to be *E. nilssoni* or *P. auritus*. Farther to the south, in the Ukraine, *E. serotinus* particularly willingly winters in various parts of buildings and it even seems to prefer these shelters to caves. The group of these 3 species, in which we may probably include also *B. barbastella*, is distinguished by its great resistance to low temperatures and relatively dry air. These species are often observed to winter in the coldest parts of caves, close to the entrance, where they are exposed to great fluctuations in microclimate, e.g., a drop in temperature to below 0° C. This characteristic makes it also possible for them to find shelters suitable for hibernation out of deep underground cavities. However, even the members of such resistant species as *E. serotinus* often perish in masses by frost or of exhaustion during hard winters (ABELENTSEV et al., 1956).

Four species of the genus *Myotis* wintering in caves in this country have greater demands as regards microclimatic conditions of hibernation and they worse tolerate falls of temperature and, especially, those in the humidity of the air. These species are not, as a rule, met with in caves with a temperature lower than +2° C and a humidity of the air lower than 85—100 %; when moved to places having a lower humidity of the air, they show symptoms of desiccation of their extremities and membranes and soon die. Hence, the possibilities of hibernation of these species are associated with more favourable conditions than in the case of the first group of bats and their dependence on underground shelters is greater. So far, the reliable reports on finding some members of the genus *Myotis* wintering in other places than caves are limited to KUZYAKIN'S (1950) mention of a specimen of *M. mystacinus* found in December in a cleft log in the mill in the village of Bukmakino (Kirov Province and KURSKOV'S (1958) observation of several specimens of *M. daubentoni* and *M. nattereri* in the cellars and vaults of houses in western Byelorussia. Bats of the species *M. mystacinus* were seen wintering in pigsties in neighbouring Finland (KAISILA, 1956).

The wintering of most of the species both in farm buildings and in dwelling houses and, especially, in old castles, churches and monasteries is known from North Europe, where the climate is more or less similar (RYBERG, 1947). Here, too, the greatest diversity is shown by the winter lodgings of *P. auritus* and *E. nilssoni*. The species of the genus *Myotis*, more sensitive than the previous ones, are encountered chiefly in cellars, vaults and other well insulated underground shelters. Numerous bat species take shelter in caves as commonly as in old buildings in neighbouring Poland; (KOWALSKI, 1955; HARMATA, 1962) and Germany (EISENTRAUT, 1937; NATUSCHKE, 1960).

Probably, it does not happen by chance that wintering bats are particularly often found in man-made shelters, among which I also include artificial caves.

At present most of the northern species of bats have become semisynanthropic to the extent that they are more frequently encountered in the proximity of human abodes than under natural conditions. Undoubtedly, this phenomenon has brought about great changes in the range, abundance and biology of many species, remarkably increasing their possibilities of finding of both summer and winter hiding places. Nevertheless, in north-eastern Europe the living conditions are more severe, the density of populations is smaller and the landscape reveals fewer signs of human interference than in the west. Consequently, the original winter quarters of natural origin are of as great importance to bats as they were in the past. Otherwise, we should have to assume that the bats managed to colonize the greater part of the European territory of the U.S.S.R., nearly completely devoid of natural caves, only very recently, following man and his economic activity in these areas. This, however, disagrees with a number of facts, especially with the frequent finds of subfossil bony remains of „cave" species and the above-mentioned slight morphological differences between the east- and west-European populations of some species, which indicates a long period of their isolation.

The bats wintering in natural shelters (except for caves) are still rarer in this country than those inhabiting houses. There are a few reports on the wintering of small groups of bats in tree-holes, which up to recently were regarded as quite unsuitable for hibernation of these animals (KUZYAKIN, 1936). So far it has been established that *P. auritus* and, probably, *E. nilssoni* may winter in tree-holes, but most of the bats found in them have not been identified. In view of the severe climate of the central and northern part of the Soviet Union it seems hardly probable that the tree-holes are of major importance as places of successful mass hibernation.

According to fairly numerous records of eye-witnesses, bats may sometimes be found in screes or in deep crevices of steep banks, where they penetrate as far as the non-freezing layers of earth. In none of these cases the species of the wintering specimens could be identified except for one in which I found a frozen *P. auritus* in a caved-in cleft in a steep bank of the Volga (Tatar A.S.S.R.). In Finland, where the climate is similar, KAISILA (1956) suggests the possibility of hibernation of bats in rock crevices, in which the high humidity and moderately low temperature favour hibernation. *M. mystacinus* and *E. nilssoni* (RYBERG, 1947) were found in similar conditions in Norway and Sweden. In the U.S.A. GRIFFIN (1945) and TWENTE (1959/60) also believe that bats, including the there numerous species of *Myotis*, regularly take shelter for winter in crevices and small holes in rocks.

KUZYAKIN (1950) supposes that *M. dasycneme* may winter in deep burrows of rodents, but so far there is no evidence to support his opinion.

The foregoing considerations have not been designed to belittle the significance of caves as the most convenient and preferable winter shelter of bats. In the northern and central regions of this country caves are as yet the only certain sites of their mass occurrence in winter. In the markedly milder climate

of Central and West Europe caves are also places where the greatest numbers of bats gather in winter, being uncommon in other types of shelters, and the wintering of some species out of caves has not been observed at all. Long migrations made by bats to reach underground shelters also indicate the great importance of caves to bats.

The term „stationary species" is used in this paper for the species wintering in caves only to mark that they do not leave central and northern regions of the European part of the U.S.S.R. I do not exclude long seasonal migrations within the bounds of this territory, for all northern bats regularly change summer quarters for winter ones and *vice versa*, and these quarters are often situated a long way from each other.

Roer (1960, 1962) presented a survey of all more important data on bat migrations obtained by European investigators as a result of banding. The studies of the Dutch, Belgian and Danish zoologists (Bels, 1952; Heerdt & Sluiter, 1953—1960, 1961—1962; Egsbaek & Jensen, 1963; Fairon, 1967) are the most interesting to us, because they banded the same Boreal species that winter in the caves of the central and northern regions of Russia.

It has been established that in Central Europe the longest migrations are performed by *M. dasycneme*; the distance between their winter and summer quarters in Belgium and Holland is up to 330 km., averaging about 200 km. Other species make considerably shorter migrations. Studies carried out chiefly in Holland but also in Denmark (Egsbaek & Jensen, 1963) show that only single specimens of *M. daubentoni* move away farther than 100 km. from their winter quarters in summer. No regular flights of more than 100 km. in length were recorded for *Myotis emarginatus*, *M. nattereri*, *M. mystacinus* and *Rh. ferrum-equinum* in Europe. The vast majority of *M. myotis* banded in different countries of Europe also remain within a limit of 100 km. from the locality of banding, but single specimens migrate considerably farther: up to 150 km. and, exceptionally, nearly 250 km. *M. oxygnathus* seems to behave similarly to *M. myotis*.

In literature there are no data concerning the migrations of *E. nilssoni*. Most of the specimens of *B. barbastella* banded in Germany and Austria were found in summer 10—80 km. from their winter lodgings, though 2 cases of very long migrations of this species (290 km. and 127 km.) were reported. Analogically, the greater part of the banded bats of the species *E. serotinus* were collected at a short distance from the site of banding (up to 50 km.), but here, too, 2 very long flights (330 and 145 km.) were noted. *Rhinolophus hipposideros* and *Plecotus* are, probably, the most stationary European species; in summer they usually inhabit no farther than 20 km. from their winter quarters.

Seasonal migrations, similar in length to those observed in Europe, have been recorded in bats wintering in caves in the northern United States and southern Canada (Griffin, 1940, 1945; Gifford & Griffin, 1960; Beer, 1955; Cockrum, 1955; Hitchcock, 1965; Davis & Hitchcock, 1965, and

others). The greatest length of flight of *Myotis lucifugus*, well examined in this respect, was 270 km., that of more stationary *Eptesicus fuscus* 68 km., but most of the banded specimens of both these species moved away to considerably shorter distances from the place of banding.

In addition to their great length, the migrations of bats are often characterized by a distinctly prevalent direction. However, both these characteristics vary remarkably, as the ecological conditions change. It has been stated, generalizing the habits of *M. myotis*, well known in Europe, that particularly long migrations, having as a rule a northern direction in spring, are undertaken by bats inhabiting regions poor in suitable winter shelters (North-German Lowlands, Netherlands), whereas the populations of the mountainous regions of Central Europe cover much shorter distances and show no preferable direction of migrations; they disperse radially from their winter quarters, almost uniformly in all directions (ROER, 1960). The Czechoslovakian investigators (HANAK et al., 1962) think that the short migrations of *M. myotis* without a prevalent direction should be regarded as original, peculiar to this species when, after the retreat of the glacier, it inhabited the regions of South and Central Europe abounding in caves. The northern flat portion of the present range of this species was not colonized by it till recently, when its transition to the semisynanthropic ways of living permitted the occupation of areas which lack natural caves. In autumn, however, the northern populations returned to their original habitations and thus, by degrees, they developed a genetically fixed instinct of directed migrations, corresponding to the direction of the spread of the species.

As compared with Central Europe, the central and northern regions of the Soviet Union have a more severe climate, which necessitates the existence of particularly infallible winter shelters, but, in contradistinction to other parts of Europe, here there are large areas devoid of caves fit for wintering. Judging by what has already been said above, under such conditions the migrations of bats should be marked by long distances and definite directions. So far, however, the concrete data concerning this problem are lacking. The banding of species wintering in caves in this country has been carried out to a very small extent; I may only name a small paper by KOLYUSHEV (1958), in which he presents the results of banding of *M. schreibersi* in the caves of the Transcarpathian Province of the Ukraine. A male of this species banded near the village of Glubokoe in the Uzhgorod District on June 29, 1955 was found in the state of hibernation near Miskolc in Hungary, 200 km. from the site of banding, as the crow flies, in the winter of 1956/1957. Another specimen banded near Miskolc on July 5, 1955 was collected in a cave near Glubokoe on October 7, 1956. ABELENTSEV (ABELENTSEV et al., 1956) writes that a specimen of the same species banded by him near Beregovo in Transcarpathia on September 23, 1948 was also found in Hungary, about 30 km. south-west of the place of banding on October 2, 1948. Towards the end of October 1948 this author saw a mass migration of *M. schreibersi* near the town of Mukachevo:

400—450 specimens flew in a south-western direction 2—4 m. above the ground within 40 minutes between 8 and 9 p. m. These data make us suppose that part of the Transcarpathian population of *M. schreibersi* winter in the caves of north-eastern Hungary.

Out of the more than 3000 bats of 6 species banded by me in the caves of the Leningrad Province, only 2 specimens were found out of the place of banding. A female of *M. daubentoni* banded in the Sablinskie Caves near Leningrad on November 18, 1956 was taken 84 km. west-north of this place on August 11, 1957 and a male of this species banded in the Staroladozhskie underground galleries on February 7, 1963 was found on the bank of the River Syas', 15 km. east of the place of wintering, on May 19, 1963.

Further studies are needed to show to what extent the pattern of bat migrations in Central Europe resembles that in the region under study.

III. MIGRATORY BAT SPECIES

Unlike the group of stationary species of bats discussed above, no wintering specimens of *Nyctalus noctula*, *N. leisleri*, *N. lasiopterus*, *Pipistrellus pipistrellus*, *P. nathusii* and *Vespertilio murinus* were found in the European part of the U.S.S.R. (except for the regions situated farthest to the south and south-west). KIRIKOV's (1952) report on his finding several hibernating specimens of the last species mentioned above in Kapovaya Cave in Bashkiria seems to be based on a mistake: in all the other caves examined in the southern Ural Mts. (as well as in other parts of the country) only externally similar *E. nilssoni* are encountered, but nobody has succeeded in finding a single specimen of *V. murinus*.

The observations collected so far suggest that these species actually leave the central and northern regions of the European part of the U.S.S.R. for winter and perform long seasonal flights, resembling those of birds in length. The initial basis of this opinion was the observation of ephemeral, periodical appearances of fairly large numbers of bats in spring or autumn in places in which they are otherwise completely absent or only very scarce. This phenomenon was observed by different investigators in the central regions of the country, in Povolzh'e, Byelorussia and many places of the Ukraine. The farther to the south and south-west, the later such waves of migrating bats will be watched in the autumn, the order being reversed in the spring. Particularly instructive and reliable data were collected by zoologists in the steppes of the southern Ukraine, where the bats are easy to observe owing to the fact that the number of convenient shelters is limited very much (FORMOZOV, 1927; ZUBKO, 1937; POPOV, 1941; ABELENTSEV et al., 1956). Towards the end of the summer and in the autumn bats of all the above-mentioned species, absent from these areas earlier, begin to appear regularly and in large numbers. Large groups of these bats may now be seen in a number of sites along the coasts

of the Azov and Black Seas (Odessa, Kherson, Golaya Pristan', Melitopol' and others); where rare forest plantations and inhabited areas provide the migrating bats with resting places. Simultaneously, these bats either disappear completely from the central and northern regions of the country or their numbers become extremely reduced. After the winter interval bats reappeared in the southern Ukraine in the spring to disappear soon till the autumn.

In the central part of Russia the autumn departure of bats begins relatively early, but it is protracted very much. Specimens of migrating *N. noctula* were seen near Moscow at the beginning of August (OGNEV, 1913). The naturalist and tourist P. S. KOZLOV kindly informed me that in the Vol'sk region (Saratov Province) the first migrating specimens of this species appear regularly as early as mid-July. Day by day their number increases and soon they occupy all the empty tree-holes. The mass flight lasts for a fortnight and by degrees it dies out completely in August. The last single specimens of *N. noctula* (probably males) are met with in the Moscow (OGNEV, 1913) and Voronezh (PANYUTIN, 1963) Provinces in the first decade of September. According to POPOV (1960), who carried out observations for many years, in Tataria the last specimen was found in the second decade of September.

KURSKOV (1962, 1965) writes that in north-eastern Byelorussia *N. noctula* disappears as early as the beginning of August, whereas in south-western Byelorussia (Białowieża Forest) it is still present in September and disappears entirely as late as the third decade of this month. In the steppes of the southern Ukraine the passage of this species begins at the end of July and the beginning of August, but they appear in masses in mid-August and in the second half of this month up to the second decade of September. An evening appearance of *N. noctula* may be observed in north-eastern and central parts of the Ukraine up to the beginning or even middle of October and in the western and south-western regions to the very end of this month (ABELENTSEV et al., 1956).

The dates of departures of other species are not equally well known. According to LIKHACHEV (1961) in the Prioksko-Terrasnyi Reserve (Moscow Province) the numbers of *P. nathusii* begin to decrease considerably from mid-August; the last specimens were observed, in dependence on the weather in the summer, from August 24 to September 15. Only single males, which depart somewhat later than the females, remain in the reserve to the beginning of September. From the Voronezh Reserve *P. nathusii* also departs more or less at the same time (V. P. DMITRIEVA, personal communication). The latest date of finding of a specimen of this species in the Volzhsko-Kamskii Region is August 18. In the delta of the Volga (Astrakhan' Reserve) an intense passage of *P. nathusii* was observed by Y. A. ISAKOV (personal communication) in the middle of September. In the Ukraine the autumn migration of this species begins in the first decade of August and in its southern regions it lasts till the first decade of November.

Bats of the species *P. pipistrellus* begin to leave the forests of the Voronezh Reserve in the first decade of August, somewhat earlier than the previous

species. Adult females disappear directly after the termination of lactation and moulting and the young bats linger until the end of the second decade of this month (V. P. DMITRIEVA). KURSKOV (1962) writes that the autumnal departures of *P. pipistrellus* begin in Byelorussia at the end of July and they too, end in the first half of August. In the Ukraine the autumnal migration of this species is observed at the same time as or somewhat earlier than that of *P. nathusii*; in the northern and central regions an increase in the number of specimens caused by their influx from the north begins at the end of July and in the first days of August, whereas they disappear here completely in the first decade of September and, in the south, as late as mid-October.

According to V. P. DMITRIEVA, members of the species *V. murinus* start flying away from the forests of the Voronezh Reserve earlier than any other species of bats. At first, towards the end of July, males and females, at least one year old fly away followed by the young, and the last single bats are occasionally met with up to the end of August. During his observations, conducted for many years, POPOV (1960) saw a specimen of this species in Tataria at the latest on September 11 and STROGANOVA (1954) found these bats in their summer quarters in the Volgograd Province to the end of August. In western Byelorussia (KURSKOV, 1965) the departures terminate at the end of this month. The first migrating specimens of *V. murinus* were observed in the southern Ukraine (Askaniya-Nova) at mid-July, but large groups of these bats occur in August and at the beginning of September. In the Carpathians (Stanislav Province) their passage was noted in the first days of October.

The flight of *N. leisleri* lasts from July to September in the southern Ukraine. No bats of this species will be seen in this area later than the first decade of September. *N. lasiopterus* on migration may be seen in the Lower-Dnieper Lowlands from August to November.

The autumnal departure of bats from their summer quarters is usually preceded by moulting and the regrouping of summer colonies: adult females separate from the young and fly away before them. It is interesting that in *N. noctula* and *P. nathusii* the mating season begins when the bats have not yet departed their summer quarters, while *P. pipistrellus*, *V. murinus* and *N. leisleri* are considered to begin mating during their migration or after the bats have reached their winter shelters. Accordingly, the males of the first two species are the last to leave their summer quarters. The mating behaviour of *N. noctula* has been described in detail by PANYUTIN (1963) and HEERDT & SLUITER (1965); a similar phenomenon was observed also in *P. nathusii* by V. P. DMITRIEVA.

According to ABELENTSEV et al. (1956), *N. noctula* migrates singly in the autumn, apart from other specimens of this species, which it joins only for day's rest.Such periodical aggregations may number up to a thousand specimens. On the other hand, migrating bats of the species *P. pipistrellus* were seen to fly in small flocks of 5—6 individuals each, the distance between particular individuals being 2—3 m. These observations are, however, in-

compatible with the simultaneous disappearance of whole colonies as well as with the common records of large flocks of bats migrating even by day both in the autumn (STADLER, 1922; FINCK VON FINCKENSTEIN & SCHAEFER, 1934; BAUER, 1955b) and in the spring (KAGAL'NITSKII, 1960).

Bats do not seem to hurry during their autumnal migrations and they stop at places to rest and feed. PANYUTIN (1968) calculated that the mean rate of migration of the banded specimens of *N. noctula* was 20—26 km. per 24 hours in 4 cases and only in 1 case it amounted to 44 km. per 24 hours. Since the calculation was based on the assumption that the bats went on migration directly after banding and that the way covered by them was a straight line, the actual rate was higher. The mean rate of migration of a banded specimen of *P. nathusii* was 23 km. per 24 hours. An uncommon rate of migration was noted in a *V. murinus* (band No. X-892124) banded on August 10, 1959 and caught 360 km. farther to the south as early as August 12, 1959. This observation differs so much from all the other results that it causes some doubt.

The dates and order of appearance of bats in the spring are not so well known as those for autumnal departures. Migrating specimens of *N. noctula* are observed in the southern Ukraine (Osipenko) from mid-March to the third decade of April. Near Kiev this species usually appears at the end of March or at the beginning of April, in the Voronezh Reserve the first individuals can be seen in the first half of April, earlier than any other species (LAVROV, 1953), but the bulk of their population come as late as the end of April and the beginning of May (PANYUTIN, 1963). KUZYAKIN'S long observations (1950) indicate that *N. noctula* appears in the Moscow region from the 20th to the 22nd of April independently of the spring weather. KURSKOV (1962) gives a later date for this species; according to his data, the forests of Byelorussia fill with the members of this species about the middle of May. In contradistinction to the departures, which proceed by degrees, the period of spring migrations is here considerably reduced; these bats can occupy the whole territory of Byelorussia within a few days.

Migrating *P. pipistrellus* appears in the Lower-Dnieper Lowlands at the end of March. The flight lasts here for 2—3 days, afterwards the members of this species disappear till the end of summer. They reach the northern Ukraine from the beginning to the middle of April. *P. nathusii* arrives at the same time or somewhat earlier; it is present in the southern Ukraine at the end of February or at the beginning of March, in the Kiev Province a month later, and near Moscow (Prioksko-Terrasnyi Reserve) at the beginning or in the middle of April. *N. leisleri* returns to its summer quarters at the very end of April and at the beginning of May and so a little later than the other species. LAVROV (1953) reports that in the Voronezh Reserve the mass spring flight of all the bat species falls in the third decade of April and, if the weather is fine, it proceeds rapidly, taking 2—3 nights altogether. The changeable, cold and windy weather causes that the flight lasts long and is hardly perceptible.

In addition to direct observations in the field, the investigations carried

out by the method of banding have provided unambiguous evidence of long seasonal migrations of bats. The first data of this sort were published by German authors, who conducted the banding of the specimens of *N. noctula* wintering in Dresden in 1934—1939 (EISENTRAUT, 1937; MEISE, 1951). Nearly all the later achievements in this field are owed to the banding applied recently on a large scale by Soviet zoologists mainly in the Voronezh Reserve and at the field station in the Białowieża Forest.

All the information obtained so far on the long migrations of bats banded in this country or found in it is summarized in Table II.

Most information based on recaptures concerns *N. noctula*, and for this reason this species is chiefly discussed below. The material that I have at my disposal is very heterogeneous. Most of the specimens banded were recaptured not in the year of banding, but several years later. As it is unknown where the given specimen spent all the time when it wore the band, its finding does not elucidate the course of its single migration. Such data must be treated very cautiously, because several adult males and females were found out of the place of banding in the spring-summer season (PANYUTIN, in litteris), which proves that bats not always return to the same places where they lived in the previous year. Besides, the vast majority of the bats may have been, judging by the dates of recaptures, on their way to or from the winter quarters. Nevertheless, the distribution of all the localities where the banded specimens have been restored, plotted on the maps (Figs. 2—3), allows the statement that the bats of the European part of the U.S.S.R. (at any rate, those from the areas west of the Volga) winter in Central and South-Eastern Europe, including the Caucasus. The interesting report of KAGAL'NITSKII (1960), who saw a huge flock of bats (as I suppose, *N. noctula*) flying over the sea between the coasts of the Crimea and Turkey in a north-eastern direction in spring, indicates that the bats may fly over the Black Sea and winter in Asia Minor.

No distinct differences have as yet been found between the routes of particular species. It is, however, striking that all the long flights of the banded specimens of both the species of *Pipistrellus* led to the eastern part of the Balkan Peninsula and not a specimen of those banded in the Voronezh Reserve (Fig. 3) was found south of the place of banding, in the Crimea and Ciscaucasia, where most of the banded specimens of *N. noctula* were recaptured. In this connection POPOV'S (1941) presumption is worth mentioning, according to whom, starting from the lower course of the Dnieper, along which the distinct route of flights of different bat species runs, the ways of migrations of the genera *Nyctalus* and *Pipistrellus* diverge. The former tend over Karkinitskii Bay to the Crimea and the latter fly south-west along the coast of the Black Sea. I cannot decide to what extent this supposition is right. Neither is it supported by ABELENTSEV *et al.* (1956) in the monograph of the Ukrainian bats, because the number of recaptures of the banded members of the genus *Pipistrellus* is not great and the distribution of the sites of recaptures may be governed by incidental factors.

Bats from different summer quarters seem to have different routes of migration and winter in different regions. Thus, *N. noctula* from the north-western area of this country probably winters in Central Europe (southern and central Germany, Czechoslovakia, Hungary and Austria), whereas its Voronezh population fly away to the Black-Sea regions (Caucasus, Crimea, Bulgaria, perhaps Romania, Greece and Turkey). KAMENEVA and PANYUTIN (1964) pronounce decidedly for this opinion, in which they are joined by KURSKOV (1965); they think that a few main „migration streams" can be distinguished in the European part of the U.S.S.R. In my opinion, however, such decisive conclusions are premature, because they are based on too scanty material, even so far as *N. noctula*, best known of all, is concerned.

The data from the Voronezh Reserve suggest that most of the specimens of *N. noctula* wander from it in S and SSE directions towards the Caucasus in the autumn (15 recaptures), to a smaller extent in a SSW direction towards the Crimea (7 recaptures), and quite a small number of these bats fly due south-west towards the Balkan Peninsula (3 recaptures). These 3 main directions distinguish themselves clearly on the diagrammatic map in Figure 2, on which the localities of recaptures of banded specimens have been connected by conventional straight lines with the places of banding, though the actual ways of migration are unknown. Most of the specimens of *N. noctula* seem to fly around the Sea of Azov along its eastern and western coasts, there being no intermediate finds north of this sea. Neither is it known whether the northern Caucasus Mts. and, especially the Crimea are hibernation areas or only a transit place for most of the arriving bats.

Be it as it may, all the localities of recaptures of *N. noctula* banded in the Voronezh region, plotted on the map, form a wide fan of dispersion, which indicates that, judging from the places of hibernation, even the population of a very small territory is extremely heterogeneous.

Such extensive dispersion of the Voronezh population may have been caused by an obstacle in the route of migration in the form of the large Azov-Black Sea basin. The banding of specimens of *N. noctula* wintering in Germany (Fig. 2) showed that, in fact, the spring migrations have a very distinct north-eastern direction, though here, too, there is a dispersion of the localities of recaptures both to the sides from the prevalent direction of the migrations and as to the distance between the place of banding and that of finding banded specimens, for these distances are very various. This last characteristic is particularly distinctive of *N. noctula* in Holland: specimens banded in the summer were found from 3 to 900 km. from the site of banding in the winter.

All these facts suggest that specimens coming from different winter quarters mix constantly with each other in summer, whereas those inhabiting different areas in summer mix with each other in their winter quarters. Since the rutting season in bats lasts from autumn to spring and theoretically they can copulate both in their summer habitations and during migration, as well as in win-

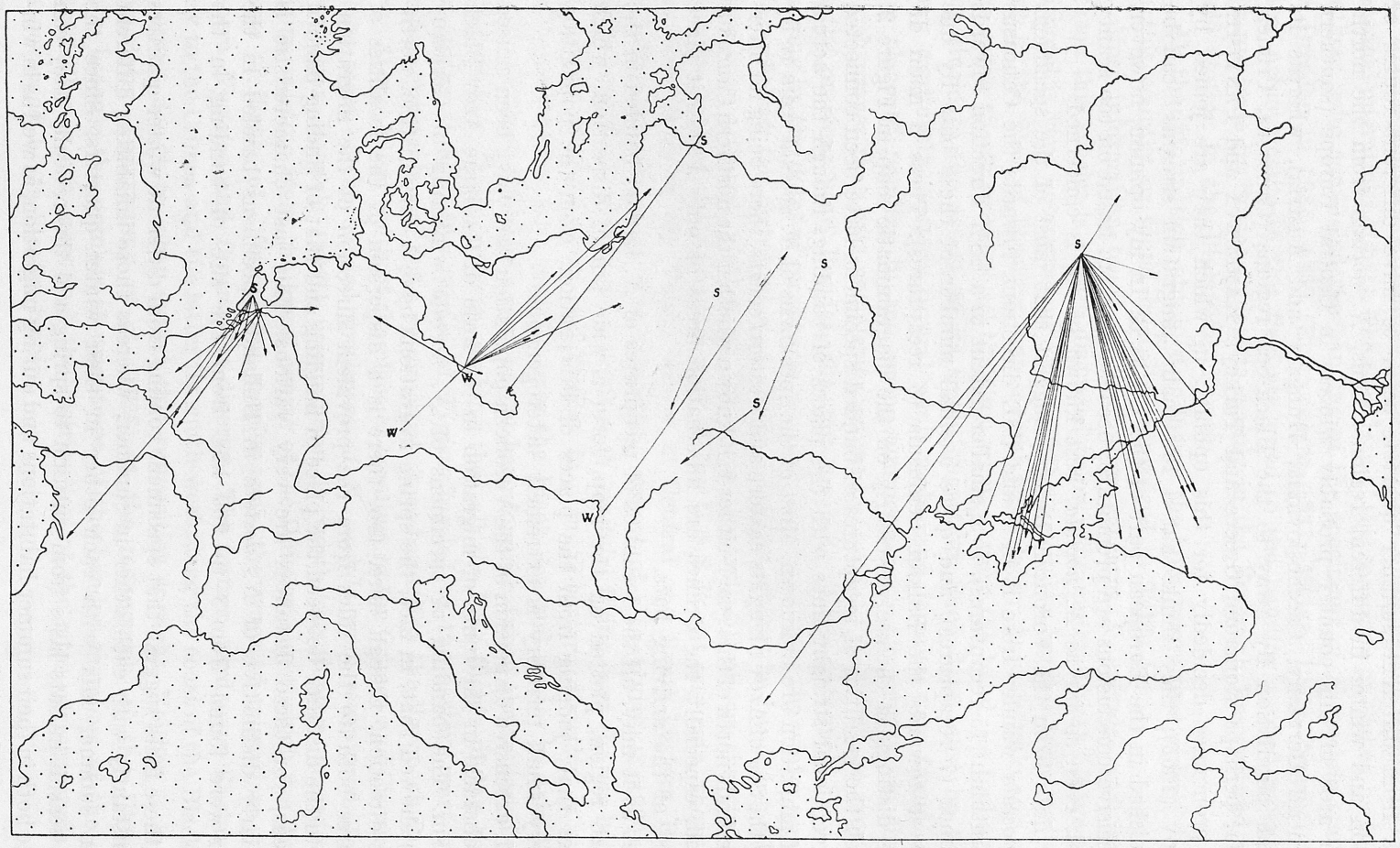

Fig. 2. A schematic map showing long flights of the banded specimens of *N. noctula* in Europe. S — banded in the summer, W — banded in the winter. Note: the longest (above 300 km.) flights of *N. noctula* banded in the U.S.S.R. or recaptured in this territory are presented in Table II in the order from north to south and from west to east (according to the site of banding); the specimens banded in the Voronezh Reserve are given in the order from east to west (acc. to the site of recapture)

ter shelters [1], this fact should prevent the formation of local isolated populations and geographical forms.

The data concerning other migratory species are very scanty. Two specimens of *V. murinus* banded in the same place (Fig. 3) were recaptured at a longer distance from each other than the length of flight of either of them. On the contrary, all the three specimens of *P. nathusii* banded in the Voronezh Reserve were caught again relatively near each other, though they had flown to a very long distance.

It is very interesting that in the migratory species the summer range of males may, as it seems, disagree with that of females. In contrast to the situation in the western and middle Asiatic parts of the range, no adult males of *P. pipistrellus* are practically met with in central Russia. According to the data obtained from the Voronezh Reserve for many years (LAVROV, 1953; KAMENEVA & PANYUTIN, 1964), no adult males of *N. leisleri* were found there either, and the females of *N. noctula* and *P. nathusii* were more numerous than the males by many times. In the Ukraine ABELENTSEV and his co-workers (1956) failed to find any adult males of *N. leisleri* at all and only extremely rarely met with those of *N. noctula* and *P. nathusii* (in the case of this last species males form 0·5% of the population). Other authors also drew attention to this fact. Only LIKHACHEV (1961) found a high proportion of males of *P. nathusii* in the forests of the Prioksko-Terrasnyi Reserve, which was undoubtedly connected with the specific nature of his investigations, covering only bird nest-boxes, where there were no colonies of females.

Moreover, KUZYAKIN (1950) tried to explain this interesting phenomenon by the hypothesis that in some species males show lower viability than females and die for the most part in the first year of life. However, in winter shelters *N. noctula* (MEKLENBURTSEV, 1935; LÖHRL, 1936; MEISE, 1951; SLUITER & HEERDT, 1966; GAUCKLER & KRAUS, 1966) as well as *P. pipistrellus* (HAAGEN & ARNOLD, 1955; BOGDANOV, 1953; DUMITRESCU & ORGHIDAN, 1963; KROCHKO, 1966a; HURKA, 1966) is represented by both sexes equally numerously, in some cases males being predominant. Males of *N. noctula* occur in large numbers not only in winter quarters, but also in summer in the proximity of the hibernation sites. BOGDANOV (personal communication) observed almost only males of *N. noctula* in Middle Asia in summer both sexes being represented in equal

[1] Another problem is that the details of reproduction of *N. noctula* are not as yet well known. The occurrence of evident rut in these bats towards the end of the summer (V. P. DMITRIEVA, personal communication; PANYUTIN, 1963; SLUITER & HEERDT, 1966) suggests that the insemination of females takes place chiefly in this season. However, in the Voronezh Reserve V. P. DMITRIEVA found only dead spermatozoids in the genital organs of females of *N. noctula* and *P. nathusii* dissected before departure. On the other hand, PANYUTIN (1963) reports that he observed pregnancy and parturition in the females of *N. noctula* caught in the same area iu the autumn and kept in the laboratory, but only in those which were left in the state of hibernation in a cold room for several months. An additional complication of this problem is the fact that the vagina of inseminated *N. noctula* is closed by a plug of connective tissue, which seems to prevent subsequent copulations.

proportions in the winter. According to KAMENEVA and PANYUTIN (1964), in the Voronezh Reserve on the average 20—30 females found fall to one male of this species. In the Crimea the same authors observed almost exclusively adult males, which in July occurred there in large colonies, numbering as many as 70 specimens (nothing like that can be seen in the north).

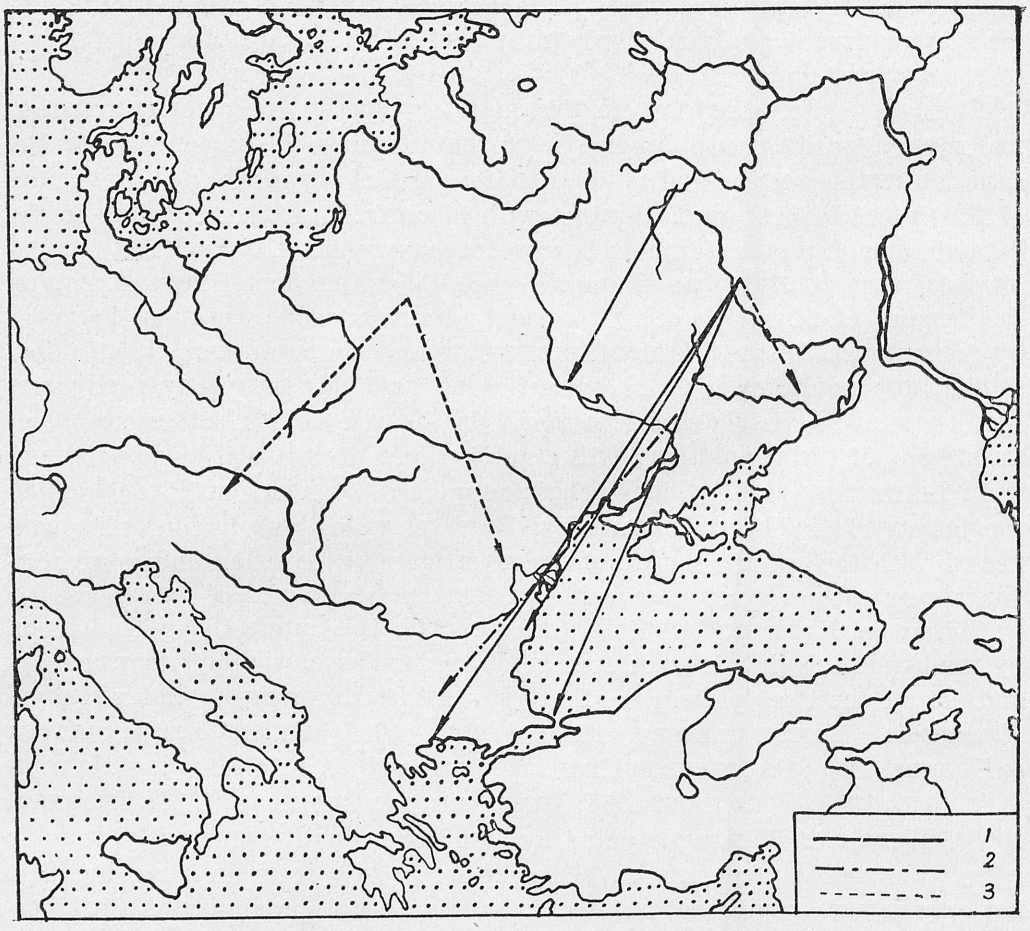

Fig. 3. Schematic map of long flights of banded bats: 1 — *P. nathusii*, 2 — *P. pipistrellus*, 3 — *V. murinus*

A similar phenomenon is observed in the Ukraine. Calculations show that in May and June adult males of *N. noctula* form hardly 2 per cent of the population in the northern and central regions, whereas in July they constitute 26 per cent in the western Ukraine. To be sure, the very investigators who described this phenomenon (ABELENTSEV et al., 1956) are inclined to attribute it not to the differences in geographical position but to that in the time of observations, i.e., the later appearance of males (not before the second half of summer) in the areas where the females reproduce.

However, this explanation cannot be accepted. V. P. DMITRIEVA (personal

communication) also informs that adult males of *P. nathusii* appear in the Voronezh Reserve chiefly towards the end of summer. According to the notes made by her personally, throughout the summer for many years, males form hardly 2·5 per cent of the catches, namely, about 0·5 per cent in the May—July period (LAVROV, 1953) and 25 per cent in August. In her opinion the problem would boil down to the fact that in summer the males live out of sight and are hard to find and next, at the beginning of the mating season, they become more active and betray their hiding places by nuptial calls. Besides, it is then that the large colonies of females begin to break up and some of them fly away, which certainly adds to the increase in the proportion of the males. PANYUTIN (1963) claims simply that in the Voronezh Reserve the numerical relation between males and females of *N. noctula* is more or less the same in the autumn as in the spring, at the time of departure as during arrivals; in the autumn the number of males does not increase, but they are easier to see when the mating season has begun. Therefore, it is more probable that males of *P. pipistrellus*, *N. leisleri*, *N. noctula* and, certainly, *P. nathusii* migrate less than females and do not reach the northern borders of their ranges or, at the most, reach them only in small numbers. It may be supposed that a considerable part of them stay somewhere out of the regions in which the females reproduce during the summer months and join the females in their winter quarters or on their way to them. The question is not clear as regards *V. murinus*; both sexes are represented in the northern part of the range, but their numerical relations are not as yet well known. Unlike the other species, the males of *V. murinus* frequently occur in the reproductive colonies of females (in the Voronezh Reserve 25 per cent of all the males collected fall to female colonies), but they oftener live in separate colonies of up to 30 specimens or quite singly.

A seasonal split of the range of a species according to the sexes has recently been described in North-American migratory *Lasiurus cinereus*. The males of this species live along the south-western coast of the United States and the females give birth to the young in the eastern and central regions of the continent (FINDLEY & JONES, 1964). Nevertheless, it must be kept in mind that also in some decidedly stationary species or populations of bats a sharp disproportion was observed in the numerical relation of sexes in summer. This is explained also by differences in biology between the sexes: females live in large colonies, which are easy to find, whereas males stay singly and secretly, are less active and, consequently, observed more rarely. Thus, great care must be taken not to come to decisive conclusions too hastily.

The long seasonal migrations of the species of the genera *Nyctalus*, *Pipistrellus* and *Vespertilio* are undoubtedly caused by the severe climate of the central and northern parts of the U.S.S.R., which does not allow them to stay in their summer habitations for winter. The possibilities of occurrence of stationary populations of these species and those of successful wintering of arrived specimens exist only in the regions situated farthest to the south and south-

west of this country. *N. noctula* and *P. pipistrellus* have been examined relatively closely in this respect.

The data presented by MEKLENBURTSEV (1935) and BOGDANOV (1950 and 1953) show that *N. noctula* and *P. pipistrellus* spend winter in Uzbekistan. Here, reed roofs, chinks in walls, spaces between window frames, etc. are their winter shelters. *N. noctula* remains occasionally in tree-holes for winter. In Tashkent the winter shelters of both these species are poorly insulated from the external environment and great drops in temperature often cause the wholesale death of the bats. Similar observations are reported by STAL'-MAKOVA (1955), who watched *P. pipistrellus* wintering in Turkmenia.

Near the town of Osh in southern Kirgizia TAGIL'TSEV (1954) found specimens of *P. pipistrellus* in small warm caves and rock crevices. Owing to unfavourable high winter temperatures of these shelters, the bats often died of exhaustion in them.

In southern Kazakhstan *N. noctula* finds similar conditions of hibernation to those in Middle Asia. In the Alma-Ata Province K. K. KLIPPERT (personal communication) observed colonies of scores of specimens in tree-holes and attics of wooden houses in the winter. *N. noctula* and *P. pipistrellus* were frequently seen wintering in Alma-Ata itself. According to KORELOV (KORELOV, 1950; AFANAS'YEV, et al., 1953), the populations of *N. noctula* living south of the 43° parallel in Kazakhstan are stationary and those inhabiting north of this parallel must migrate to the regions characterized by milder winter conditions.

In SATUNIN'S opinion (1915), *P. pipistrellus* winters in large numbers in Transcaucasia. I was informed by P. P. GAMBARYAN that the specimens of *P. pipistrellus* hibernating in Armenia were encountered in different parts of buildings in Yerevan and they were found in large numbers in deep crevices of rocks in the Vedynsk District in the winter. In the north-western Caucasus the zoologist KHONYAKINA (after KUZYAKIN, 1950) saw bats of the species *N. noctula* hibernating in deep rock crevices on the southern slope of Tsereblovaya Mt. (Caucasian Reserve). Specimens of this species wintering in the southern Crimea were found in tree-holes (KAMENEVA & PANYUTIN, 1960). Judging from the numerous finds of the specimens of *N. noctula* banded in the Voronezh Reserve, the Crimea and northern Caucasus may be the region of hibernation of the bats coming here from the central areas of chernozem of Russia.

KOZLOV (1949) writes about the probable hibernation of *P. pipistrellus* in the Crimean Reserve and KONSTANTINOV and DMITRIEVA (1962) found several sleeping specimens of this species in a narrow crevice at the entrance of Kizil-Koba Cave near Simferopol'.

Both *N. noctula* and *P. pipistrellus* as a rule hibernate in Transcarpathia, where the local populations of these species seem to be stationary (ABELENTSEV, 1950; ABELENTSEV et al., 1956; KAMENEVA & PANYUTIN, 1960; KROCHKO, 1966a). In winter these species were often met with in various parts of buildings of Uzhgorod and in the environs of Mukachevo, and *N. noctula* also in large

tree holes. These last bats aggregate into large compact masses, numbering up to 1000 specimens in their winter shelters. In the periods of severe frost many of them perish; then mass migrations of bats from the mountains into the valleys may sometimes be observed.

The data given by KROCHKO (1965, 1966b) show an interesting fact, namely, that the males strongly predominate (80 per cent) among the specimens of *N. noctula* wintering in Transcarpathia, whereas both sexes are equally numerous as regards *P. pipistrellus*.

Single specimens of *N. noctula* were found wintering in the farther east situated regions of the Ukraine (L'vov, Belaya Tserkov) and in sea towns (Kherson, Melitopol', Odessa), where the bats which come from the north may stay for long. The only record of the mass hibernation of *N. noctula* in tree-holes in the Nezhin region, Chernigov Province (VELIKANIV, 1930) has not been confirmed by anyone and is doubtful (and so are some other facts given by this author).

Out of the Soviet Union, in South, West and Central Europe, *N. noctula* and *P. pipistrellus* are considered to be species generally wintering there. Out of the neighbouring countries they were found in winter in Czechoslovakia (HANAK et al., 1962; HURKA, 1966) and Romania (DUMITRESCU et al., 1962/1963; DUMITRESCU & ORGHIDAN, 1963). No records in this respect have been obtained from Poland, but in the eastern regions of the G.D.R., as I have been informed by Prof. G. NATUSCHKE, who kindly shared his own observations with me and gave me some valuable bibliographical instructions, bats of both these species were seen many a time wintering in various parts of buildings and *N. noctula*, additionally, in tree-holes. According to RYBERG (1947), stationary populations of *P. pipistrellus* and *N. noctula* live in southern Sweden.

The hibernation regions of other migratory species are far worse known. Reliable records of wintering *P. nathusii* have been obtained only from Transcarpathia. ABELENTSEV (1950) found its specimens there, together with those of *N. noctula* and *P. pipistrellus*, in the flues and the holes between the walls and window frames of the University building in Uzhgorod. Some data indicate that this species winters in tree-holes in Transcarpathia. *P. nathusii* may hibernate in south-eastern Transcaucasia. In Lenkoran KUZYAKIN (1950) observed these bats in April and at the beginning of May, afterwards they all disappeared and their shelters were occupied by *P. pipistrellus*. Out of the Soviet Union several wintering colonies of *P. nathusii* were found in tree-holes in Germany (KLEMMER, 1953; GERBER, 1956). In Zealand (RYBERG, 1947) hibernating specimens of this species were seen in piles of planks. The finds of banded specimens of *P. nathusii* suggest that they winter in the south-eastern region of the Balkans.

N. leisleri and *N. lasiopterus* have not as yet been found in the U.S.S.R. in the winter. Y. I. KROCHKO (personal communication) saw single hibernating specimens of *V. murinus* in a tree-hole near Svalyava in Transcarpathia. A dead individual was found in a small cave near Osh in Kirgizia in winter

(TAGIL'TSEV, 1954). In winter this species was also observed in Sweden (RYBERG, 1947) and Austria (BAUER, 1954, 1955a), where it seems to hibernate in urban stone buildings.

As may be inferred from the data collected so far, the areas of hibernation of *N. noctula* and *P. pipistrellus* coincide more or less exactly, which indicates the existence of common factors controlling the behaviour of these species. Interesting results have been obtained by plotting the northernmost and easternmost hibernation places of both species on a climatic map (Fig. 4). At first I thought (STRELKOV, 1958) that the hibernation area of *N. noctula* and *P. pipistrellus* in Europe is limited by the isotherm of the mean daily temperature of January approximating to —2°— —3°, because they are generally unable to survive the cold season with still lower temperatures, as evidenced by their very high mortality-rate during frosty winters both in the southern and south-western regions of this country (see above) and abroad (RYBERG, 1947; MEISE, 1951; NATUSCHKE, 1960; ROER, 1963). For example, according to K. K. PANYUTIN (personal communication), there was such a dramatic drop in the abundance of *N. noctula* and both species of *Pipistrellus* in the Voronezh Reserve after the extremely severe European winter of 1962—63 that they have not as yet restored its original level.

However, a close analysis of this problem showed great climatic differences between the places in which bats may survive winter. In the north-east of the Balkans *N. noctula* and *P. pipistrellus* winter under more severe conditions than in Central Europe and, especially, on the coast of the Baltic Sea, and in the mountainous part of Transcaucasia (Armenia) *P. pipistrellus* stands as low a mean daily temperature of January as —6°. With respect to climate the conditions of hibernation of *N. noctula* and *P. pipistrellus* in Kazakhstan are particularly severe. In Alma-Ata, at an altitude of 840 m., the mean daily temperature of January reaches —8° and the annual number of days with a mean daily temperature of —10° and lower amounts to 30. Nowhere in Europe do bats winter in similar conditions.

The foregoing facts show that in similar severe winter climates the migratory bat species remain for winter in some parts of the range and fly away in the others. The causes of this phenomenon are not clear; it is possible that different populations are resistive to the cold to a various degree, but it may well be that the climatic differences are partly levelled owing to the differences in the behaviour and, particularly, by the choice of suitable microclimates and shelters. Thus, it becomes necessary to determine the boundary of the hibernation area of the migratory species under study as precisely as possible and to carry out a close complex analysis of the influence of all climatic elements on the bats under the extreme conditions of hibernation.

It is striking that in the areas where the hibernation of *N. noctula* is possible in so far as climatic conditions are concerned and where it actually takes place, the instances of long migrations are also known. The specimens banded in Holland in the summer (BELS, 1952; HEERDT & SLUITER, 1965; SLUITER

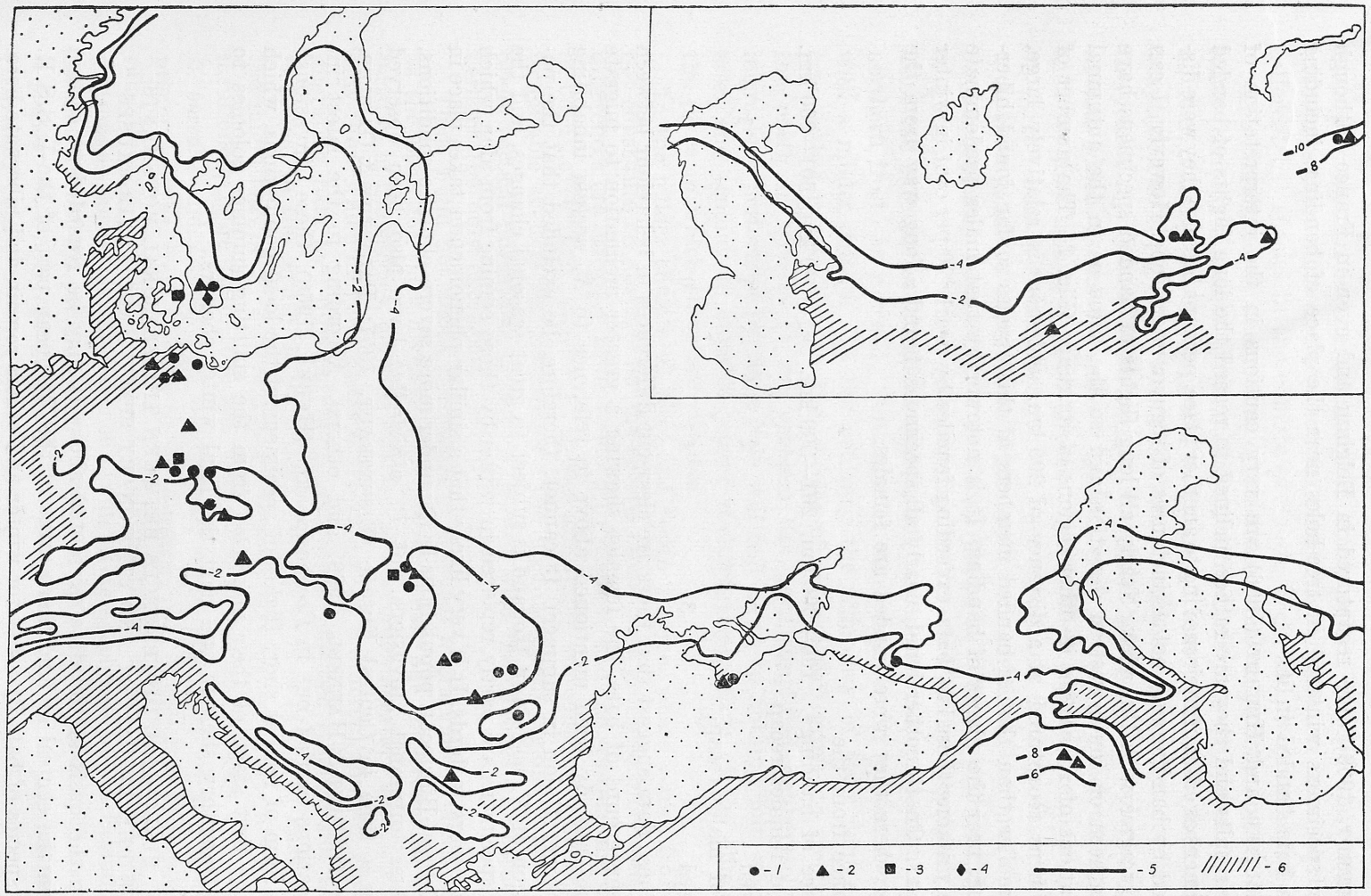

Fig. 4. The localities situated farthest to the north and north-east in which hibernating bats were found: 1 — *N. noctula*, 2 — *P. pipistrellus*, 3 — *P. nathusii*, 4 — *V. murinus*, 5 — isotherms of mean daily temperature of January, 6 — areas in which the mean daily temperature of January is 0 C or higher.

& HEERDT, 1966) were recaptured in Belgium and even in France, although other specimens wintered in tree-holes near the place of banding, including some bats banded in it.

SLUITER and HEERDT (1966) are very cautious in the interpretation of their results and they are rather inclined to regard the long flights of banded specimens as cases of their moving to another place, perhaps because they were disturbed by banding and not as instances of regular migrations. However, I can hardly agree with this view. Nearly all long flights of banded specimens have a southern or south-western direction and so the same as in the autumnal migrations of *N. noctula* in other regions of its range (Fig. 2). The number of specimens recaptured at a distance of 200 km. and more is relatively large, no smaller than that of banded members of this species so far found hibernating, near the places of banding. It is noteworthy that males predominate largely among these last bats, exceeding females by nearly 20 per cent in winter shelters. On the other hand, nearly all specimens found a long way from the place where they were banded are females.

Distance from the place of banding	100—200 km.	201—300 km.	301—500 km.	501—900 km.
No. of females recaptured	7	2	4	1
No. of males recaptured	3	1	0	0

These data suggest that there are clear-cut differences in behaviour between the sex groups of bats, the females showing a greater inclination to migrate (as has already been mentioned above in reference to *N. noctula* inhabiting the Soviet Union in summer). It cannot, therefore, be excluded that the population of *N. noctula* in Holland is subject to great seasonal changes, and the local specimens are partly replaced in winter by those coming from afar, which often occurs in birds. It is very likely that a similar phenomenon takes place in the Central-European populations living under more severe climatic conditions.

Mass autumnal „invasions" of *P. pipistrellus* have also been observed many a time in Central Europe (EISENTRAUT, 1957; PALASTHY & GAISLER, 1965; GRUMMT & HAENSEL, 1966, and others). According to the latest investigations carried out in Czechoslovakia (HURKA, 1966), these „invasions" are a form of regular short flights of specimens of the local populations, which are the first stage of their migration from the splitting summer colonies to their transitory shelters and next the final winter shelters.

IV. BIOLOGICAL DIFFERENCES BETWEEN THE SEASONAL MOVEMENTS OF THE MIGRATORY AND STATIONARY SPECIES AND THEIR CAUSES

On the basis of the data presented above it may be regarded as certain that in the central and northern areas of the European part of the U.S.S.R. some species of bats fly away for winter and others remain and hibernate here.

This phenomenon is characteristic of north-eastern Europe and connected with its severe climate. There are no such great differences in the habits of different bat species in the climate of South, West and even Central Europe.

The simultaneous occurrence of stationary and migratory species in the same territory indicates great biological differences between them. Their behaviour, varying in this respect, seems to be associated with their various adaptation to the given types of shelters. It has been generally accepted that the genera *Nyctalus*, *Pipistrellus* and *Vespertilio* belong to the ecological group of bats which, unlike the „cave" species, avoid caves and other underground shelters. Most members of this group, which is often called a group of „wood" or „tree" bats („Baumfledermäuse"), are associated through their shelters with trees (some of them perhaps also with rock crevices), but many species have secondarily been adapted to hiding places in different overground parts of human houses. Their normal winter shelters are always poorly insulated from the external environment and do not provide reliable protection against northern frost. As a result, these species must migrate for winter to regions with a milder climate. On the contrary the reliability of their winter shelters makes it possible for the species of the „cave" group to remain in the north in winter. If the problem has been simplified deliberately, the migrations performed by these bats will boil down to nothing but searching after and tending to suitable winter shelters, irrespective of the climate of the place in which these are situated.

In the milder climate of West and South Europe, where winter frost does not constitute an obstacle for the species of the first group to hibernate, these differences are certainly being reduced by degrees, and the seasonal migrations of both „cave" and „non-cave" species are simply searching after and moving to suitable shelters for hibernation. The high-mountain regions, where there occur vertical migrations of bats connected with the changes of weather, are perhaps the only exception.

Thus, I did not adopt the length of seasonal migrations of northern bats as the basis for their division into 2 main types, but the ecological characteristics of the species, defining their nature; as true migratory species I regard only those which move to places characterized by a different climate. However, migrating bats face different tasks, which are reflected (though not always, it seems) in the length of their flight. In the climate of North-East Europe the migrations of *N. noctula* and *P. nathusii* may cover, as has already been mentioned, more than 1500 km. Some North-American species *(L. cinereus*, *L. borealis* and *Lasionycteris noctivagans)* make migrations of still more surprising lengths, from Canada to the southern part of the United States (Florida, Georgia, South Carolina). A good indication of the length of these migrations is the regular appearance of migrating specimens in the Bermuda Is., separated from the continent by a stretch of 600—800 miles of open sea. Even a passage of single specimens of *L. cinereus* to Iceland was twice recorded (Hayman, 1959).

Such long migrations have not been observed in „cave" species either in Europe or in North America. As has already been shown, the migrations of these bats do not usually exceed 100—200 km., although the longest flights made by some banded specimens from their summer quarters to winter shelters, or vice versa, covered as much as 300—350 km., and one specimen of *M. schreibersi* (species marked by fast flight and an inclination for migrations) was recaptured at a distance of 550 km. from the place where it had been released after banding 4 years earlier (ROER, 1960). The long migrations, 1000 km. or more, of the typical „cave" species *Tadarida brasiliensis mexicana* from the south-western United States and northern Mexico (VILLA & COCKRUM, 1962) are an apparent exception, for these members of the tropical family *Molossidae* settled in the temperate zone not long ago, have a different type of thermoregulation from that in most northern *Vespertilionidae* and, unlike these last, are not adapted for long hibernation (HERREID, 1963a, b). This fact seems to influence their manner of behaviour; they do not change the type of shelter, but the climatic zone in which they spend winter.

A weak point of the foregoing considerations is the relativity of the division (based on the predisposition to take a special type of winter shelters) of the northern bats into „non-cave" and „cave" species. Although this division is in the principle right, it is too schematic and does not suit the great diversity of habits of these mammals.

The extreme members of the first group are the North-American migratory species *L. cinereus*, *L. borealis* and *L. noctivagans*. These species do not usually hide even in tree-holes, spending the day in the crowns of trees and shrubs. However, even these well-specialized species may sometimes be encountered in caves, though after a long stay in them they perish and the underground chambers in which they occur become true cemeteries for hundreds of specimens of both sexes and various age (MYERS, 1960).

Out of the European species, the best specialized tree-hole inhabitants, both in summer and in winter, are *N. leisleri*. They seem to be met with in other types of shelters only exceptionally (BAUER, 1954). *N. noctula* also takes shelter almost exclusively in tree-holes in summer, but on migration and in winter it often shelters in attics and chimneys, under the vaults of church domes, in unheated rooms, behind window frames, and in unprotected niches and hollows in walls. The hibernation of this species has been investigated by many authors (LÖHRL, 1936; MISLIN & VISCHER, 1942; MEISE, 1951; SKREB & DJULIĆ, 1955; PORA & ROSCA, 1955; HEERDT & SLUITER, 1965). The hibernating specimens are usually poorly insulated from the external conditions, which seems to be the cause of their tendency to aggregate into large groups, numbering up to a thousand specimens, in this period; in such compact masses it is easier for them to stand too low temperatures. The occurrence of specimens of *N. noctula* in rock crevices has already been mentioned; occasionally they are even found in caves (SCHREITMÜLLER, 1940/43; DUMITRESCU & ORGHIDAN, 1963).

P. nathusii seems to spend winter in shelters similar to those of *N. noctula*, i.e., in tree-holes and buildings. *P. pipistrellus* is a considerably less „tree" species and it shows more plasticity so far as choice of shelters is concerned. In a great part of its range this species has changed its ways of living for the synanthropic ones to a great extent and has lost its connection with natural shelters almost completely. In winter it shelters preferably in old buildings (churches, cloisters, fortification towers, etc.) but, unlike the previous species, it may often be met with also in underground shelters. Nevertheless, hibernation of this species in caves is not a typical phenomenon; its specimens are generally found here in small numbers hidden in fissures in the ceiling and walls of the part situated just inside the entrance, where the temperature and relative humidity of the air are lower and less constant than those farther inside the cave (see, e.g., HAAGEN & ARNOLD, 1955). However, under certain circumstances the hibernation of this species may take place in conditions quite typical of the „cave" species proper. Special attention should be given to the fact, described recently by DUMITRESCU and ORGHIDAN (1963), of hibernation of this species in Sura-Mare Cave in Romania, where, according to rough calculations, 80,000—100,000 specimens of both sexes flock together. This huge number and some slight morphological differences in relation to the local specimens suggest that a great part of this population consists of specimens which have come from afar. However paradoxical it appears, the winter colony of bats in Sura-Mare Cave must be regarded as one of the largest in Europe, though the main species represented in it, as a rule, avoids caves. (None the less, North-American *Pipistrellus subflavus*, a close relative of the European species, hibernates in caves only.)

In addition to *P. pipistrellus*, some specimens of *N. noctula*, were also found in this cave. Large amounts of subfossil bone remains of this species, the age of which has been determined to be 2900 years, were also encountered in another cave in Romania (DUMITRESCU et al., 1955).

On the other hand, out of the European species only *M. schreibersi*, the *Rhinolophidae* and most species of the genus *Myotis* may be regarded as true „cave" species, which choose only deep caves or other similar artificial undergrounds, characterized by a constant, moderately low temperature and high relative humidity. I have already emphasized the fact that many species hibernating in caves — *P. auritus*, *E. nilssoni*, *B. barbastella*, *E. serotinus* and, in the temperate zone of North America, *Eptesicus fuscus* — may spend winter also in other shelters, e.g., shelters with climatic conditions similar to those in which the „non-cave" species hibernate. A particularly striking example in this respect is *E. serotinus*, which leads an exclusively synanthropic life in Europe and only with great difficulty can be included in the group of bats hibernating underground; in caves it always occurs in small numbers and is usually observed in parts situated close to the entrance. This ecologically plastic group of species, which, according to the local conditions, may hibernate successfully in both under- and overground shelters, holds something like an

intermediate position between the cave-inhabitants proper and tree-hole inhabitants.

It is very possible that many biologically differing species, especially *N. noctula*, the genus *Pipistrellus*, *V. murinus*, *E. nilssoni* and several species of *Myotis* hibernate in identical shelters, e.g., rock crevices, but because of their inaccessibility this supposition is based on only single finds. Considerably more often this phenomenon may be observed in inhabited houses and farm buildings. No doubt, the passage to partial or full synanthropism made the original specialization of the bats with respect to shelters less clear and brought the shelters of these species, which cannot be met with together under natural conditions, closer to each other. Dwelling houses and farm buildings, diversified in respect of conditions, provide shelters to immemorial inhabitants of tree-holes, rock crevices and caves. For example, in southern Sweden (RYBERG, 1947) some churches are inhabited all the year round by so diverse species as *N. noctula*, *P. pipistrellus*, *V. murinus*, *E. nilssoni*, *E. serotinus*, *P. auritus*, *B. barbastella* and 2 species of *Myotis*. The definite and specific requirements as to the site of hibernation, peculiar to each species or group of biologically related species can undoubtedly be observed here, too (HARMATA, 1962, and others). Nevertheless, it is difficult to make a sharp division of bats on the basis of their winter shelters; only the extreme variants, linked together by a number of intermediate forms, ecologically plastic and very labile as regards the choice of shelters for hibernation, are easy to demarcate from each other.

A closer analysis of the differences in winter shelters is made difficult by the fact that owing to insufficient knowledge of the ecological and physiological characteristics of particular species it is unknown what they are associated with now and what they were associated with in the past, and when their specific stereotype of behaviour arose. The stenotopicallity of typical cave species may be explained by their specific demands with regard to microclimatic conditions of hibernation in connection with their great sensitivity to humidity and low temperature. In the light of the foregoing facts it is, however, hardly possible to consider the avoidance of underground shelters by the „tree" bats to be an expression of their physiological incompatibility with the microclimates of caves; this may, at the most, be true of American *Lasiurus* and *Lasionycteris*, which are probably incapable of true hibernation.

These considerations refer especially to the relatively mild climate of Central Europe, although some local differences in the behaviour of bats may be seen even here. In the severe climatic conditions of the central and northern regions of the European part of the U.S.S.R. the potentially high lability of bats in so far as choice of hibernation sites is concerned cannot be fully actualized. All the „non-cave" species fly away for winter and such species as *P. pipistrellus* behave as if they had not „discovered" the possibility of hibernation in the caves situated near their summer quarters, though in their traditional hibernation areas they often use caves for this purpose.

As has already been mentioned, little is known of the sites of wintering of the species from the „cave" group in this country, and the available data are one-sided, as they are based almost exclusively on the finds of specimens in caves. Many ecologically plastic species probably pass more and more to the cave ways of living, both literally (i.e., they are encountered more frequently and in relatively larger numbers in caves proper) and figuratively (i.e., they find well-insulated shelters for winter, especially underground ones, such as deep crevices in steep banks, burrows, deep cellars, etc., in which the conditions of hibernation are similar to those in caves).

None the less, our stationary species sometimes hibernate in shelters (not exclusive even of tree-holes) which in remote winter quarters are used by migratory species. For example, *E. serotinus* keeps practically the same habits in winter in the central and north-western Ukraine as in Central Europe, though it may be included among the „non-cave" species nearly equally well as migratory *P. pipistrellus*.

These facts prove that, though the manner of staying of bats in the north is undoubtedly connected with their specialization for the given type of shelters, this circumstance by itself is not sufficient to explain the necessity of undertaking long migrations by some species and the ability of other species to survive winter in the north. The variety of adaptations of bats to the climate of the north will remain ununderstandable until other physiological and ecological properties of theirs, the origin and history of the spread of particular species, and the general history of formation of the northern bat fauna have been included in the study.

V. CONCLUSIONS

1. Sixteen species of hibernating bats have been found in the caves of the European part of the U.S.S.R. (Fig. 1, Table 1). So far unexplained clear-cut differences in the quantitative and qualitative composition of the wintering bats, depending on a given part of the country, are observable. On the basis of repeated observations of hibernating bats, among other places, on the northern borders of their geographical distribution, and having taken into account a number of intermediate facts, all these species are regarded as comparatively stationary in this territory. This does not exclude their local seasonal migrations from summer quarters to winter ones and *vice versa*.

2. Six Boreal species (*M. dasycneme*, *M. daubentoni*, *M. mystacinus*, *M. nattereri*, *P. auritus* and *E. nilssoni*), widely distributed all over central and northern Russia, cannot winter only in caves, because these are very rare here and completely lacking at places. Apparently, these species must spend winter also in some other, so far unknown, shelters.

3. Six species — *N. leisleri*, *N. noctula*, *N. lasiopterus*, *P. pipistrellus*,

Table I

List of bats' species hibernating in the caves investigated in the European part of the Soviet Union

Administrative district	No.	Cave name	List of species and approximate numbers of bats																References
			Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	*Myotis myotis*	*Myotis oxygnathus*	*Myotis bechsteini*	*Myotis emarginatus*	*Myotis nattereri*	*Myotis mystacinus*	*Myotis dasycneme*	*Myotis daubentoni*	*Plecotus auritus*	*Plecotus austriacus*	*Barbastella barbastella*	*Eptesicus nilssoni*	*Eptesicus serotinus*	*Miniopterus schreibersi*	
Bashkirskaya ASSR	1.	Kapova								a			b			a?			KIRIKOV, 1952
	2.	Kyzyl-Yar							a				c						PANYUTIN, pers. commun.
Chelyabinsk Prov.	3.	Serpievskaya								a			a			b			STRELKOV, 1958
	4.	Kurgazak (Kukshinskaya)									b		a						„ „
	5.	Laklinskaya														b			„ „
Sverdlovsk Prov.	6.	Skaz											b						BOL'SHAKOV, pers. commun.
	7.	Shakhta 49 (Sarana)														a			BOL'SHAKOV, 1966
	8.	Druzhba							a	a	a	a				a			PANYUTIN, pers. commun.
	9.	Arakaevskaya								a		b	b			b			PANYUTIN, pers. commun.

	10.	Malaya Arakaevskaya											a			b			PANYUTIN, pers. commun.
	11.	Kourovskaya											a			a			PANYUTIN, pers. commun.
	12.	Smolinskaya								a	d	d							STRELKOV, 1958
	13.	Gost'kovskaya											b						,, ,,
	14.	Sokharevskaya														a			,, ,,
	15.	Galleries at the Sos'va River								a	a		a			a			KUZNETSOV and KOZLOV, 1958
Perm Prov.	16.	Pashiiskaya														a			VORONOV, 1951
	17.	Div'ya								c		a	a			a			STRELKOV, 1958
Tatarskaya ASSR	18.	Syukeevskaya											a						POPOV, 1960
Gor'kii Prov.	19.	Bornukovskaya											c						PANYUTIN, pers. commun.
	20.	Icholkovskaya								+						+			PANYUTIN, pers. commun.
Moskva Prov.	21.	Kamkinskie and S''yanovskie caves							a	b	a	a	a						STRELKOV, 1958; PANYUTIN, pers. commun.
Karel'skaya ASSR	22.	Pert-Navolokskaya								a		a							STRELKOV, 1958
Leningrad Prov.	23	Staroladozhskie caves								b	d	d	a						,, ,,
	24.	Sablinskie caves							b	c	a	a	c			a			,, ,,
	25.	Borshchevskie caves								a		a	b						,, ,,
	26.	Rozhdenstvenskaya											a			a			,, ,,
	27.	Galleries of the „Ploskoe" works										a	a			a			,, ,,
	28.	Korpovskie caves							a	a		a	b			a			,, ,,
Estonian SSR	29.	Laagri								a	a	a	b			a			LING, 1953; POOTS, 1953, 1956
	30.	Akh'ya														a			LING, 1953; POOTS, 1953, 1956

Table I (continued)

Administrative district	No.	Cave name	List of species and approximate numbers of bats																References
			Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	*Myotis myotis*	*Myotis oxygnathus*	*Myotis bechsteini*	*Myotis emarginatus*	*Myotis nattereri*	*Myotis mystacinus*	*Myotis dasycneme*	*Myotis daubentoni*	*Plecotus auritus*	*Plecotus austriacus*	*Barbastella barbastella*	*Eptesicus nilssoni*	*Eptesicus serotinus*	*Miniopterus schreibersi*	
	31.	Arukyula											a						Ling, 1953; Poots, 1953, 1956
	32.	Piuza								a		a	a			a			Ling, 1953; Poots, 1953, 1956
Voronezh Prov.	33.	Galievskaya									a	a							Strelkov, 1958
	34.	Belogorskaya and Kostomarovskie caves											a						„ „
	35.	Divnogorskaya											a						„ „
	36.	Shatrishchenskaya									a								„ „
	37.	Kalachevskaya										a	a						„ „
Belgorod Prov.	38.	Kholkovskaya										a	a						„ „
	39.	Shmarnovskaya										a	a						„ „
Sumy Prov.	40.	Safronievskaya										a	a						„ „
Kiev Prov.	41.	Group of caves in the vicinity of Kiev								a		b	a		a		b		Abelentsev et al. 1956; Abelentsev and Panyutin pers.

																					commun. ; TATARINOV, 1952, 1956, 1962 ; KROCHKO, 1964
L'vov Prov.	42.	Cave at Penyaki							a		a	a									Same refers to items 42—70
	43.	Medovye caves			a		a		a	a		a	a		b		b				
	44.	Belogoritsy caves													a						
	45.	Catacombs at Stradch and Kozlinka			a		a		a	a		a	a		a		a				
Ivano-Frankovskaya Prov.	46.	Mokraya		a	c																
	47.	Stalaktitovaya		a	c							a			a						
	48.	Kolodtsy caves		a	a										a						
Ternopol' Prov.	49.	Trovertinovskaya		a	a										a						
	50.	Sinyak		a	a								a		a		a				
	51.	Entuziastov		a	a							a	a				a				
	52.	Ugrynskaya		a	a							a	a								
	53.	Verteba (Bil'che Zoloto)		d	a					a		a	a				a				
	54.	Krishtaleva		b	b								a								
	55.	Vetrovaya (Korolivskaya)		d	b								a								
	56.	Ozernaya		b	b								a								
	57.	„Na Khomakh"		a	a								a		a						
Khmel'nitskaya Prov.	58.	Karmalyuka		a																	
Chernovtsy Prov.	59.	Ducha		a																	
Zakarpatskaya Prov.	60.	Galleries at Solotvino	a	a	a	a		a						a			a	a			
	61.	Gallery at the Delovoe		a	a	a											a	b			
	62.	Khrustal'naya and Druzhba	a	a	b	b											a	a			

Table I (continued)

Administrative district	No.	Cave name	List of species and approximate numbers of bats																References
			Rhinolophus ferrumequinum	*Rhinolophus hipposideros*	*Myotis myotis*	*Myotis oxygnathus*	*Myotis bechsteini*	*Myotis emarginatus*	*Myotis nattereri*	*Myotis mystacinus*	*Myotis dasycneme*	*Myotis daubentoni*	*Plecotus auritus*	*Plecotus austriacus*	*Barbastella barbastella*	*Eptesicus nilssoni*	*Eptesicus serotidus*	*Miniopterus schreibersi*	
	63.	Greben' and Mol. Kamen'	c	a	c	a				a							a	a	
	64.	Gallery in the Chornaya Gora at the Vinogradovo	a	a															
	65.	Beer house vaults in Muzhievo	b	b	a	a		a						a			a	b	
	66.	Galleries near Beregovo	c	b	a	a	a	a						a	a		a	b	
	67.	Galleries at Glinyanets	a	a	a									a			a	a	
	68.	Tunnel at Kol'chino	c	a	c	b		a	a					a				c	
	69.	Galleries at Dolanin	b	b	a	a								a			a	a	
	70.	Cave at Glubokoe	b	b	c	d		a	a					a	b			c	
Moldavian SSR	71.	Sakharna		c		d					a	a	a		a		a		Lozan and Skvortsov, 1965; Averin and Lozan, 1965; Lozan, and Skvortsov pers. commun.

	72.	Sokol				a						a								Same refers to
	73.	Buchushka				a							a							items 72—79
	74.	Zhelobok		c		a	a				a	b	a				a			
	75.	Braneshty		c	a	a	a		a	a		b	b	a	a		b			
	76.	Krikovo		c	a		a			b	a	b	a		a		a			
	77.	Malye Mileshty		b	a		b			b		b	b		d		b			
	78.	Braila		a						a		a	a							
	79.	Bychok	a	d						b	a	a	a	a			c			
Odessa Prov.	80.	Odessa catacombs								b	a	a	b				a			Volyanskii, 1967
Krymskaya Prov.	81.	Kyzyl-Koba	b	a											a		a			Konstantinov and Dmitrieva, 1962; Dmitrieva and Panyutin, pers. commun.
	82.	Stavrikaiskaya	a																	Same refers to items 82—90
	83.	Zmeinyi grot	a	a																
	84.	Caves in Basman Mountain	b	a											a					
	85.	Eni-Sala	c																	
	86.	Beshuiskie Kopi	a												a					
	87.	Manaiskie caves	a																	
	88.	Ak-Manaiskie	b			d				a										
	89.	Adzhi-Mushkaiskie	b			c														
	90.	Cave in Opuk Mountain				a														
Astrakhan Prov.	91.	Gallery in Bogdo Mountain																	a	Strelkov, 1958

Note: The number of hibernating bats has been estimated approximately on the basis of the highest number of specimens found in a cave during one visit: a — fewer than 10, b — fewer than 50, c — more than 50, d — more than 100 specimens, + — number unknown.

P. nathusii and *V. murinus* — make regular seasonal migrations, comparable in respect of distance with those of birds.

In central Russia the autumnal passage of bats begins at mid-July and lasts till mid-September, in southern regions — till the end of October. The summer quarters are usually abandoned first by adult females and only then by the young ones, in *N. noctula* and *P. nathusii* by adult males, too. Judging from the data obtained from banding the average rate of autumnal migrations is hardly 20—40 km. per day.

Mass spring arrivals begin in the central part of the country in the third decade of April and at the beginning of May. The spring migration period is reduced and, if the weather is favourable, lasts 2—3 nights.

4. The migratory species inhabiting the European part of the U.S.S.R. winter in Central and South-East Europe and in the Caucasus Mts. (Figs. 2—3, Table 2). No clear-cut differences have as yet been observed between the routes of migration of different species. A species seems to have various migration routes and may winter in geographically various areas, according to the fact where the summer quarters of this population are situated: *N. noctula* from the north-western regions of the U.S.S.R. hibernates in Central Europe, whereas the population from the Voronezh Province fly away to the Black Sea regions. The data obtained in the Voronezh Reserve suggest that the composition of a population, even that of a very small area, is not homogeneous as regards hibernation sites (Fig. 2).

5. No adult males of *P. pipistrellus* and *N. leisleri* are encountered in central Russia in the summer and a marked quantitative predominance of females appears in *N. noctula* and *P. nathusii*. It may be supposed that the males of these species (at least of the first two of them) live out of the breeding areas of the females and do not join them until they have started on migration or arrived in winter quarters.

6. The areas in which the migratory species of bats winter are extremely diverse in respect of their climate. In the Baltic countries and Central Europe the approximate boundary of the hibernation area of *N. noctula* and *P. pipistrellus* is the January isotherm of −2°— −3°C, in the Balkan Peninsula and in the mountainous regions of Transcaucasia bats hibernate at lower temperatures, and in southern Kazakhstan they content themselves with as low a mean daily temperature of January as −10°C (Fig. 4).

7. An important circumstance that causes differences in habits between the stationary and migratory species is their varied adaptation to different types of winter shelters. The migratory species of the genera *Nyctalus*, *Pipistrellus* and *Vespertilio* usually avoid caves and other underground shelters and hibernate in tree-holes, different crevices, overground parts of houses, etc. These shelters are poorly insulated from the external temperature, and for this reason these species must migrate for winter to regions with a milder climate. The stationary species, as a rule, winter in caves and other similar underground

Table II

Long-distance flights of bats banded in the Soviet Union or recaptured there

No.	Ring number	Species	Sex	Age	Date		Place name		Distance flown in km	References
					of ringing	of recapture	of ringing	of recapture		
1.	A-1495	*N. noctula*	?	?	12. III. 1935	9. VI. 1935	Dresden (Germany)	Near Tel'shyai (Lithuania)	750	EISENTRAUT, 1937; MEISE, 1951
2.	F-89025	„ „	?	?	21. VIII. 1949	26. IX. 1949	Riga (Latvia)	Czeske Lipy (Northern Bohemia)	930	LAVROV, 1955
3.	MKB-X-13788	„ „	?	?	16. XII. 1964	29. V. 1966	Nürnberg (S. Germany)	Gvardeisk distr., Kaliningrad Prov.	890	Dr. ROER (FGR), pers. commun.
4.	26254	„ „	F	ad	3. III. 1959	?. VIII. 1960	Budapest (Hungary)	Ivenets, Minsk Prov.	850	KURSKOV, 1965
5.	X-724998	„ „	F	?	23. VII. 1958	10. V. 1960	Osipovichi distr., Mogilev Prov.	Velikii Glubochek distr., Ternopol' Prov.	600	KURSKOV, 1962; 1965
6.	F-129145	„ „	F	ad	12. VIII. 1953	16. VII. 1954	Belovezhskaya Pushcha Reserv., White Russia	Near Rzeszow (SW Poland)	350	KURSKOV, 1962, 1965
7.	P-60068	„ „	F	subad	23. VII. 1960	29. VIII. 1961	Voronezh Reserv., Voronezh Prov.	Nizhne-Chirskaya distr., Volgograd Prov.	460	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
8.	F-545868	„ „	M	?	7. VIII. 1955	3. IX. 1958	Voronezh Reserv., Voronezh Prov.	Peshchanokopskoe distr., Rostov Prov.	675	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
9.	P-60516	„ „	F	subad	16. VIII. 1960	5. IX. 1960	Voronezh Reserv., Voronezh Prov.	Belaya Kalitva distr., Rostov Prov.	420	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
10.	F-588048	„ „	M	subad	12. VIII. 1959	15. IX. 1959	Voronezh Reserv., Voronezh Prov.	Novo-Aleksandrovskaya distr., Stavropol' land	750	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
11.	P-75090	„ „	F	ad	24. V. 1961	13. IV. 1962	Voronezh Reserv., Voronezh Prov.	Kavkaz distr., Krasnodar land	720	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
12.	P-75002	„ „	F	ad	23. V. 1961	18. IV. 1962	Voronezh Reserv., Voronezh Prov.	Gul'kevichi distr., Krasnodar land	730	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
13.	P-60349	„ „	F	subad	14. VIII. 1960	?. VII. 1961	Voronezh Reserv., Voronezh Prov.	Labinsk distr., Krasnodar land	820	Bureau of Ringing of the USSR
14.	F-73543	„ „	F	ad	29. VI. 1949	?. V. 1951	Voronezh Reserv., Voronezh Prov.	Novocherkassk distr., Rostov Prov.	485	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
15.	P-60022	„ „	F	subad	20. VII. 1960	20. IV. 1961	Voronezh Reserv., Voronezh Prov.	Bogaev distr., Rostov Prov.	510	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
16.	F-305406	„ „	F	ad	3. V. 1957	15. IV. 1960	Voronezh Reserv., Voronezh Prov.	Adler distr., Krasnodar land	900	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
17.	P-60459	„ „	F	ad	17. V. 1962	2. VI. 1963	Voronezh Reserv., Voronezh Prov.	Rostov na Donu	520	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
18.	P-60307	„ „	F	subad	10. VIII. 1960	28. VIII. 1960	Voronezh Reserv., Voronezh Prov.	Leningrad distr., Krasnodar land	800	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
19.	P-75352	„ „	F	ad	17. VII. 1961	8. IV. 1962	Voronezh Reserv., Voronezh Prov.	Dinskaya distr., Krasnodar land	730	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
20.	F-58130	„ „	F	ad	30. VIII. 1947	17. X. 1950	Voronezh Reserv., Voronezh Prov.	Goryachii Klyuch distr., Krasnodar land	800	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
21.	P-60046	„ „	M	subad	22. VII. 1960	16. V. 1961	Voronezh Reserv., Voronezh Prov.	Abinskaya distr., Krasnodar land	760	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
22.	F-574709	„ „	M	subad	19. VII. 1963	8. IV. 1966	Voronezh Reserv., Voronezh Prov.	Kirovskoe distr., Krym Prov.	800	Bureau of Ringing of the USSR
23.	F-58079	„ „	F	juv	6. VIII. 1947	28. V. 1956	Voronezh Reserv., Voronezh Prov.	Belogorsk distr., Krym Prov.	830	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
24.	F-60923	„ „	F	ad	26. VI. 1947	4. V. 1953	Voronezh Reserv., Voronezh Prov.	Nizhnegorskii distr., Krym Prov.	800	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
25.	F-305925	„ „	F	ad	13. VIII. 1957	3. X. 1958	Voronezh Reserv., Voronezh Prov.	Zuya distr., Krym Prov.	840	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
26.	P-19678	„ „	M	subad	11. VIII. 1958	23. X. 1959	Voronezh Reserv., Voronezh Prov.	Simferopol' distr., Krym Prov.	850	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
27.	P-75764	„ „	M	subad	3. IX. 1961	13. V. 1962	Voronezh Reserv., Voronezh Prov.	Bakhchisarai distr., Krym Prov.	890	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
28.	P-75197	„ „	F	ad	13. VI. 1961	11. V. 1963	Voronezh Reserv., Voronezh Prov.	Chaplinka distr., Kherson Prov.	760	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
29.	P-19901	„ „	M	juv	14. VIII. 1958	15. IX. 1958	Voronezh Reserv., Voronezh Prov.	Rovnoe distr., Kirovograd Prov.	690	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
30.	P-60376	„ „	M	subad	16. VIII. 1960	17. IX. 1960	Voronezh Reserv., Voronezh Prov.	Lyubashevka distr., Odessa Prov.	800	KAMENEVA & PANYUTIN, 1960; PANYUTIN, 1968
31.	F-305917	„ „	F	subad	13. VIII. 1957	3. I. 1961	Voronezh Reserv., Voronezh Prov.	Pazardzhik (SW Bulgaria)	1600 (2347)	BURESH & BERON, 1962; PANYUTIN, 1968
32.	G-81121	*P. pipistrellus*	F	ad	28. VI. 1939	8. IX. 1939	Pereshchepino distr., Dnepropetrovsk Prov.	Near Plovdiv (S. Bulgaria)	1160 (1697)	POPOV, 1941; BURESH & BERON, 1962
33.	X-762297	*P. nathusii*	F	ad	23. VII. 1958	22. VIII. 1958	Prioksko-Terrasnyi Reserv., Moskva Prov.	Borisopol' distr., Kiev Prov.	680	LIKHACHEV, 1961
34.	X-700743	„ „	M	subad	23. VII. 1958	?. XI. 1958	Voronezh Reserv., Voronezh Prov.	Near Stambul (Turkey)	1500	KAMENEVA & PANYUTIN, 1960
35.	X-956096	„ „	F	ad	24. V. 1961	8. IV. 1963	Voronezh Reserv., Voronezh Prov.	Kavalla (Greece)	1600	PANYUTIN, 1968
36.	Y-260847	„ „	M	subad	12. VII. 1956	?. V. 1958	Voronezh Reserv., Voronezh Prov.	Near Varna (Bulgaria)	1300 (1950)	BURESH & BERON, 1962; PANYUTIN, 1968
37.	X-892124	*V. murinus*	F	?	10. VIII. 1959	12. VIII. 1959	Voronezh Reserv., Voronezh Prov.	Mal'chevskaya distr., Rostov Prov.	360	PANYUTIN, 1968
38.	X-800907	„ „	M	ad	11. VI. 1959	4. X. 1959	Belovezhskaya Pushcha Reserv., White Russia	Fokshany, Galati distr. (E. Rumania)	800	KURSKOV, 1961
39.	X-84455	„ „	M	ad	14. VII. 1956	10. VIII. 1961	Belovezhskaya Pushcha Reserv., White Russia	Bruck a. d. Mur, Styria (Austria)	850	KEPKA, 1962; KURSKOV, 1965

1) The distances in straight lines from the site of banding to those of recaptures given in the paper by BURESH and BERON (1962) are considerably greater than the distances calculated on the basis of the medium-scale tables of equivalent and equi-angular projections. In the present table, to render comparison possible, I give the distances calculated in the second manner, which is besides used by all authors, and the figures of the Bulgarian investigators are offered in brackets.

2) In the paper by BURESH and BERON (1962) a bat banded in the Voronezh Reserve (No. 260847) and recaptured in Bulgaria was, through no fault of these authors, identified erroneously as *Myotis mystacinus*, whereas, in fact, it was a young specimen cf. *Pipistrellus nathusii* (PANYUTIN, 1968).

shelters, well insulated from frost. Their seasonal migrations boil down to the action of searching after shelters and moving to them, regardless of the climate of the place in which these shelters are situated.

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STRESZCZENIE

Na terytorium europejskiej części Związku Radzieckiego znaleziono dotąd ponad 90 jaskiń, w których zimują nietoperze, łącznie 16 gatunków (rys. 1, tab. I).

Najszczegółowszej analizie poddano 6 gatunków borealnych: *M. dasycneme*, *M. daubentoni*, *M. mystacinus*, *M. nattereri*, *P. auritus* i *E. nilssoni*, zimujące w surowym klimacie środkowych i północnych regionów europejskiej części Związku Radzieckiego i Uralu. Z nich najpospolitszy, spotykany zimą w prawie wszystkich jaskiniach, jest *P. auritus*; prawie równie pospolity jest *M. daubentoni*, a w północnej połowie kraju — *E. nilssoni*. Pozostałe gatunki spotyka się znacznie rzadziej; charakterystyczna dla nich jest sporadyczność i skrajna nierównomierność ilościowego rozmieszczenia w badanych jaskiniach. Najrzadszym z zimujących gatunków jest *M. nattereri*.

Mimo całej jednolitości składu zimujących nietoperzy istnieją wyraźne różnice co do stopnia zasiedlenia przez nie jaskiń, zależnie od okolicy kraju:

wszystkie 6 podanych gatunków bardzo silnie reprezentowane są zimą w jaskiniach północno-zachodnich regionów; prawie równie obfite są one w jaskiniach Uralu. Bardzo mało nietoperzy jest w jaskiniach regionów Centralno-czarnoziemnych i Powołża. Przyczyny tych różnic są na razie niejasne.

Wszystkie gatunki nietoperzy zimujące w jaskiniach środkowej i północnej części Związku Radzieckiego należy uważać za stosunkowo osiadłe, tj. pozostające na zimę na obszarach swego letniego pobytu. Dowodzi tego nie tylko wielokrotne znajdowanie ich zimą w jaskiniach, m. in. na północnych granicach ich rozmieszczenia geograficznego, ale i fakty pośrednie. Jednak mała ilość jaskiń i słabe zasiedlenie większości z nich przez nietoperze dowodzą wyraźnie, że ich kryjówki zimowe nie ograniczają się tylko do jaskiń i większość ich spędza zimę w jakichś innych, nie znanych jeszcze kryjówkach.

6 gatunków nietoperzy: *N. noctula*, *N. leisleri*, *N. lasiopterus*, *P. pipistrellus*, *P. nathusii* i *Vespertilio murinus* — porzuca na zimę środkowe i północne regiony europejskiej części Związku Radzieckiego, wykonując wielkie, sezonowe wędrówki. Dowodzą tego bezpośrednie obserwacje w terenie i wyniki obrączkowania (rys. 2—3, tab. II). Populacje z europejskiej części ZSRR odlatują na zimę do środkowej i południowo-wschodniej Europy (włącznie z Kaukazem) oraz, być może, do Małej Azji. Wydaje się, że *N. noctula* pochodzące z rozmaitych obszarów ich letniego areału mają także rozmaite szlaki migracyjne i rozmaite obszary zimowisk: populacje z północno-zachodniej Rosji i krajów nadbałtyckich spędzają zimę w Europie środkowej, podczas gdy populacje z Centralno-czarnoziemnych regionów odlatują w okolice wybrzeży M. Czarnego. Wszystkie punkty powtórnych znalezień *N. noctula* zaobrączkowanych w rezerwacie Voronezh tworzą szeroki „wachlarz rozlatywania się" (rys. 2); to dowodzi, że — sądząc po regionach zimowania — populacja nawet bardzo małego terytorium może być nadzwyczaj niejednolita.

W środkowych i północnych okolicach europejskiej części Związku Radzieckiego zupełnie się nie spotyka dorosłych samców *P. pipistrellus* i *N. leisleri*, zaś u *N. noctula* i *P. nathusii* samce są wielokrotnie rzadsze od samic. Możliwe, że samce tych gatunków, a zwłaszcza dwóch pierwszych, wędrują mniej niż samice i przebywają w lecie poza obszarami rozmnażania się ostatnich; przyłączają się zaś do nich dopiero na zimowiskach lub w drodze do nich.

Przyczyny sezonowych wędrówek gatunków z rodzaju *Nyctalus*, *Pipistrellus* i *Vespertilio* leżą w surowym klimacie Europy Wschodniej. Możliwości istnienia w naszym kraju osiadłych populacji tych przelotnych gatunków, tj. ich zimowania, istnieją tylko w Zakarpackim okręgu Ukrainy, na Krymie i na Kaukazie, a na wschodzie — w południowym Kazachstanie i Środkowej Azji. Granica obszarów, gdzie możliwe jest zimowanie przelotnych gatunków jest klimatycznie niejednolita (średnia miesięczna t. stycznia waha się od —10°C w południowym Kazachstanie do —1—0°C w Europie środkowej).

Istotna biologiczna różnica między osiadłymi a przelotnymi gatunkami nietoperzy polega na odmiennej ich specjalizacji do rozmaitych typów kryjówek. Pierwsze zimują w kryjówkach dobrze izolowanych, zwykle pod-

ziemnych, drugie — w kryjówkach słabo izolowanych od środowiska zewnętrznego. Stąd gatunki rodzaju *Nyctalus*, *Pipistrellus* i *Vespertilio* zmuszone są wędrować na zimę do regionów o łagodniejszym klimacie, podczas gdy osiadłe gatunki „jaskiniowe" mało zależą od klimatu okolicy, w której spędzają zimę. Dlatego wędrówki sezonowe gatunków „jaskiniowych" zwykle nie przewyższają 100—300 km, podczas gdy gatunki przelotne corocznie przemieszczają się na odległości 1000 km i więcej. Jednak trudno jedynie rozmaitą specjalizacją do różnych typów kryjówek zimowych wytłumaczyć konieczność dalekich wędrówek dla jednych gatunków nietoperzy i możliwość przeżywania zimy na północy u innych.

РЕЗЮМЕ

На территории Европейской части СССР к настоящему времени известно более 90 различных пещер, в которых обнаружены зимующие летучие мыши 16 видов (Рис. I, Табл. I).

Наиболее подробно рассматривается 6 бореальных видов — *Myotis dasycneme*, *Myotis daubentoni*, *Myotis mystacinus*, *Myotis nattereri*, *Plecotus auritus*, *Eptesicus nilssoni*, которые зимуют в условиях сурового климата средней и северной полосы Европейской части СССР и Урала. Самым обычным из них, который встречается здесь зимой почти во всех пещерах, следует считать ушанов, почти столь же обычны водяные ночницы, а в северной половине страны — северные кожанки. Прочие виды встречаются значительно реже, для них характерна спорадичность и крайняя неравномерность в количественном распределении по обследованным пещерам. Самый редкий зимующий вид — ночница Наттерера.

При всей однородности состава зимующих животных имеются заметные различия в степени заселенности ими пещер в разных частях страны. Все 6 перечисленных видов очень полно представлены зимой в пещерах северо-западных областей, почти столь же богаты зимовки летучих мышей в пещерах Урала. Очень слабо заселены летучими мышами оказались пещеры Центрально-черноземных областей и Поволжья. Причины этих различий пока не ясны.

Все виды летучих мышей, найденные зимой в пещерах средней и северной полосы СССР, следует считать относительно оседлыми, т.е. остающимися на зиму в области летнего обитания. Это доказывается не только их многократными находками зимой в пещерах, в том числе у северных границ ареалов, но и рядом косвенных признаков. Однако малое количество имеющихся пещер и слабая заселенность большинства из них летучими мышами определенно указывает, что места зимовок рукокрылых не могут ограничиваться только пещерами и большинство животных проводит зиму в каких-то иных, неизвестных пока убежищах.

6 видов летучих мышей — *Nyctalus noctula, Nyctalus leisleri, Nyctalus lasiopterus, Pipistrellus pipistrellus, Pipistrellus nathusii, Vespertilio murinus* — покидают на зиму среднюю и северную полосу Европейской части СССР, совершая дальние сезонные миграции. Это доказывается непосредственными наблюдениями в поле и результатами кольцевания животных (табл. 2, рис. 2—3). Летучие мыши из Европейской части СССР улетают зимовать в Центральную и юго-восточную Европу (включая Кавказ) а так же, возможно,в Малую Азию. Создается впечатление, что рыжие вечерницы из разных частей своего летнего ареала имеют разные области зимовок и пути миграций: животные из северо-западных частей России и Прибалтики проводят зиму в Центральной Европе, в то время как вечерницы из центрально-черноземных областей улетают в районы, прилегающие к побережью Черного моря. В совокупности все встречи окольцованных в Воронежском заповеднике рыжих вечерниц (рис. 2) показывают широкий „веер разлета"; это свидетельствует, что по признаку места зимовки население даже локальной территории может быть крайне неоднородно.

В средней и северной полосе Европейской части СССР взрослые самцы нетопырей-карликов и малых вечерниц практически не встречаются вовсе, а у рыжих вечерниц и нетопырей Натузиуса самцы по численности во много раз уступают самкам. Можно предполагать, что самцы этих видов, по крайней мере первых двух, менее склонны к миграциям, чем самки, задерживаются на летние месяцы вне области размножения последних и присоединяются к самкам лишь на местах зимовок или на пути к ним.

Причины сезонных миграций вечерниц, нетопырей и двуцветных кожанов связаны с суровым климатом Восточной Европы. Условия для существования оседлых популяций и зимовки перелетных особей этих видов в нашей стране имеются лишь в Закарпатской области Украины, в Крыму, на Кавказе, а на востоке — в южном Казахстане и Средней Азии. Граница области, где возможна зимовка перелетных видов, климатически неоднородна (среднемесячная температура января меняется от —10°С в южном Казахстане до —1 —0°С в Центральной Европе).

Существенное биологическое различие между оседлыми и перелетными видами летучих мышей заключается в их разной специализации к типу убежища. Первые зимуют в хорошо защищенных, преимущественно подземных убежищах, вторые — в слабо изолированных от наружной среды. Поэтому вечерницы, нетопыри и двуцветные кожаны вынуждены перемещаться на зиму в области с более мягким климатом, в то время как оседлые „пещерные" виды мало зависят от климатических особенностей той местности, где проводят зиму. Соответственно, сезонные миграции „пещерных" видов обычно не превышают 100—300 км, в то время как перелетные виды ежегодно перемещаются на расстояния до 1000 и более км. Однако одной только разной специализацией в выборе зимних убежищ трудно объяснить необходимость дальних миграций для одних летучих мышей и возможность переживать зиму на севере для других.

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PAŃSTWOWE WYDAWNICTWO NAUKOWE—ODDZIAŁ W KRAKOWIE—1969

Nakład 710+90 — Ark. wyd. 4,75 — Ark. druk. 3+1 wkładka — Papier ilustr. kl. III, 70×100, 80 g
Zam. 432/69 Cena zł 16.—

DRUKARNIA UNIWERSYTETU JAGIELLOŃSKIEGO W KRAKOWIE