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Seasonal Migrations and Population Dynamics of the Long-Eared Owl (*Asio otus*, Strigiformes, Strigidae) Based on 60-Year-Long Trapping and Ringing in the Eastern Baltic

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Abstract—Based on the results of trapping and ringing long-eared owls on the Curonian Spit in Kaliningrad oblast in the amount of 3391 individuals during 1957–2016, the population numbers, the migration routes and wintering grounds, the age structure, and the causes of bird death were studied. The overall efficiency of ringing was 3.01%, but the number of ring recoveries decreased significantly over time. The annual number of long-eared owls captured varied widely over 60 years, from 1 to 365 individuals. The oscillations were wave-like in nature and showed different amplitudes. In this regard, we discuss the numbers of long-eared owls and the degree of their territorial mobility in relation to abundance variations in the voles as their main food objects. Among the migrating owls, immature individuals (83%) and females (65%) predominated, and the longevity record was 16 years and 3 months. Of all 102 ring recoveries, only 16 birds were found alive. The main direction of flights in autumn was from south to west. The largest number of ring recoveries indicating the main flyways and wintering grounds came from Germany and neighboring countries at latitudes of 50°–54°N. Some ring recoveries indicate the origins of the populations of long-eared owls migrating through the Curonian Spit, since subsequently they were found is Lithuania, Latvia, Belarus, Finland, as well as on different territories of Russia, from Leningrad oblast to Tatarstan.

Keywords: migration routes, wintering grounds, age structure, ringing efficiency, population origin

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INTRODUCTION

The long-eared owl is a common species of owl, widespread in the temperate zones of Eurasia and North America. Being the most numerous of the Palearctic owls, the long-eared owl depends in its diet throughout its range on the density of populations of mouse-like rodents, primarily voles of the genus *Microtus*. It is known that long-eared owls start breeding in much larger numbers than usual during the years of outbreaks of voles (Korpimäki and Norrdahl, 1991; Korpimäki, 1992; Priklonskii and Ivanchev, 1993; Houston, 2005; Volkov et al., 2009, 2009a; Saurola, 2014). A number of reports on the life of owls indicate that the long-eared owl is a sedentary bird in many parts of its range and, most often, leads a nomadic lifestyle in autumn and winter. Northern populations are true migratory birds. However, during years of very high abundance of voles in breeding areas, they do not make long journeys (Dementiev, 1951; Eck and Busse, 1973; Pukinskii, 1977; Cramp, 1985).

The long-eared owl, along with other bird species, is regularly caught and ringed on the Curonian Spit (Eastern Baltic) by employees of the Rybachiy Biological Station of the Zoological Institute of the Russian Academy of Sciences. The data obtained on the migrations of birds with maps of their movements based on the results of the first decade of work were published, including for the long-eared owl (Payevsky, 1971). Subsequently, materials on the abundance of this species during migration and the main directions of its migrations until 1985 in comparison with the data of ringing in other regions were also published (Belopolskii, 1975; Sapetina, 1991; Dobrynina, 1994). Over the next 35 years, new information has been obtained on fluctuations in the annual number of migratory owls, the results of their lifetime examination and the pattern of territorial distribution of migrants in Europe. These new materials were the reasons for writing this article.

MATERIALS AND METHODS

The Curonian Spit is a narrow strip of land separating the Curonian Lagoon from the Baltic Sea. The spit

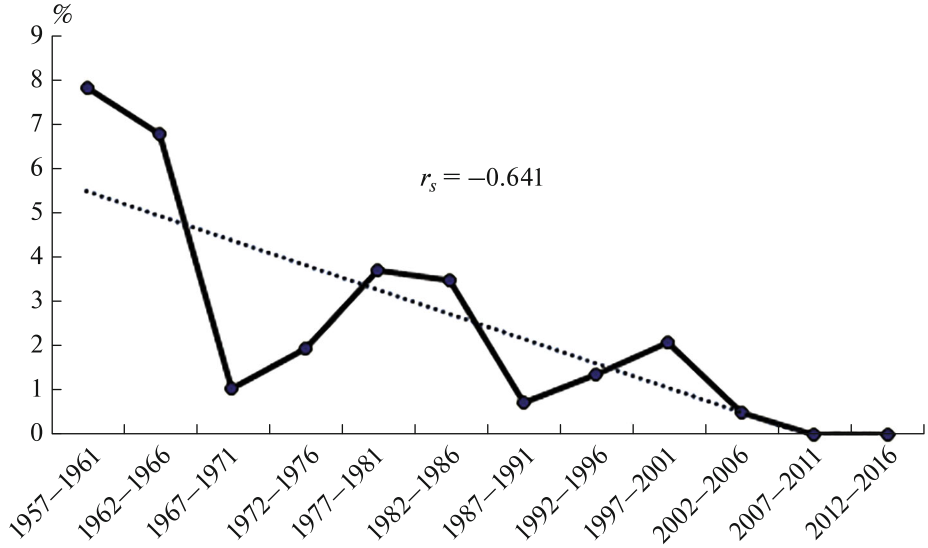

Fig. 1. Dynamics of the percentage of ring recoveries from ringed long-eared owls over 60 years.

is elongated in the direction from northeast to southwest, which coincides with the main direction of bird migration in the Eastern Baltic. Trapping and ringing of birds by the team of the Rybachiy Biological Station of the Zoological Institute of the Russian Academy of Sciences has been carried out on the spit since 1957 to the present in two places: at the Fringilla field station (55°05′ N, 20°44′ E) and at Cape Rossitensky (55°09′ N, 20°51′ E). In the first of them, birds are caught in great Rybachiy traps; in the second one, they are caught with mist nets. The Rybachiy traps for catching migratory birds, their design and mechanism of action were described in detail (Dolnik and Payevsky, 1976). The traps operate for 7 months of the year, from late March to early November. Working around the clock, the traps effectively catch owls at night. The duration of action of each trap (which had an invariable design) varied very slightly over the years, consisting of several days at the beginning of spring and the end of autumn trapping. The capture and ringing of birds are accompanied by their lifetime examination, determination of sex and age, as well as standard measurements of wing length and body weight. Since 1991, the age and sex of long-eared owls began to be determined based on plumage color characteristics (Holt, 2016; Demongin, 2016).

Lists of all quantitative data on trapping, ringing, and ring recoveries have been published (Payevsky, 1971; Bolshakov et al., 1999, 2001, 2005, 2008; Shapoval et al., 2017). In these publications, the coordinates of the points of location, the time elapsed since the day of ringing, the distance and azimuth are given with information about recoveries. We used these data to analyze the territorial distribution of migrants.

Population trends were calculated by regression analysis over time series, where one set of variables is time indicators (months or years), and the other is the number of birds caught. The effectiveness of the ringing method was calculated using the Spearman rank coefficient, and the analysis of the territorial distribution of different groups of migratory owls by ring recoveries was carried out using the χ^2 test and the Wilcoxon test (Hollender and Wolf, 1983; Sokal and Rohlf, 1998).

RESULTS

Ringing Efficiency

In just 60 years, from 1957 to 2016, 3391 long-eared owls were trapped and ringed on the Curonian Spit, and there were 102 'recoveries'of our rings, i.e., reports on the discovery of ringed owls, which make it possible to judge the range and direction of migratory movements as well as their longevity. The obtained 102 reports on the finds of long-eared owls with our rings account for 3.01 ± 0.01% of the 3391 ringed individuals. The calculation of the dependence of the number of ring recoveries on the number of ringed birds was carried out for 5-year periods, since there were years with zero number of ring recoveries. The result for the Spearman rank coefficient showed a moderate relationship ($r_s = -0.641$, $n = 12$, $p < 0.01$); i.e., the number of ring recoveries significantly decreased over time. In graphical form, this dependence is more obvious (Fig. 1).

Dynamics of Number of Migrants

The annual number of long-eared owls caught on the Curonian Spit fluctuated sharply over the course of 60 years, from 1 to 365 individuals. These changes were wavelike in nature and showed different ampli-

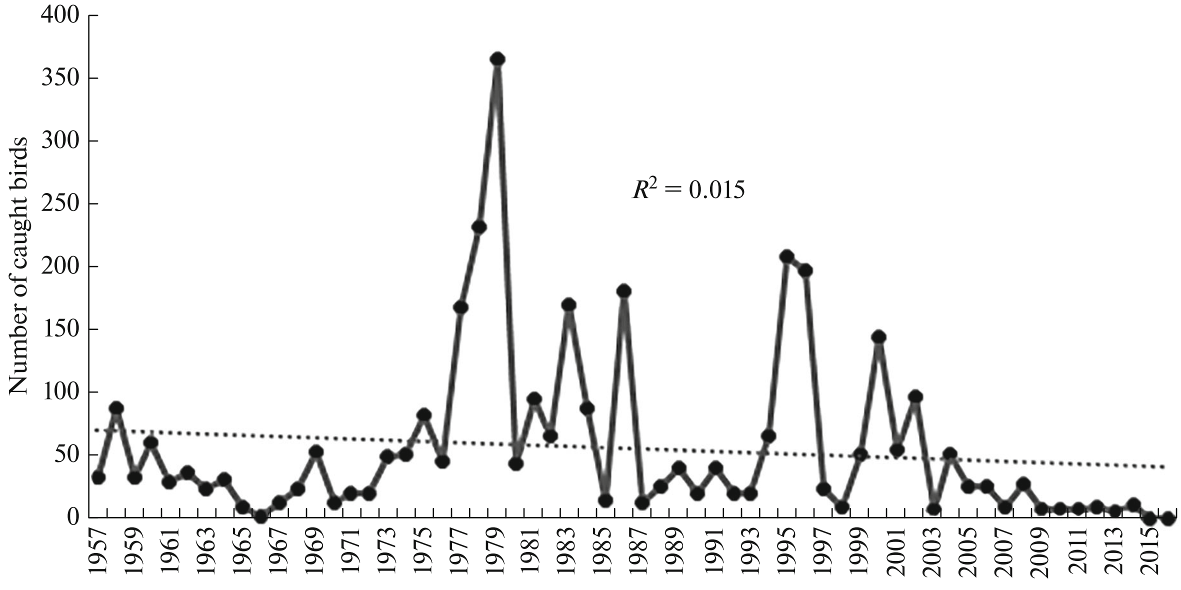

Fig. 2. The number of long-eared owls caught and ringed on the Curonian Spit in different years for 60 years, 1957–2016.

tudes (Fig. 2). Despite the huge interannual differences in the number of owls caught, the coefficient of determination $R^2 = 0.02$ indicates the absence of a significant long-term change in abundance.

Age and Sex Composition of Migrants

The wing-length measurements of male and female long-eared owls largely overlap, which made it impossible to determine the sex composition by the wing length in all individuals. The wing length varied from 259 to 317 mm, but birds with a wing length from 287 to 299 mm could be of either sex. Since the age and sex of long-eared owls on the Curonian Spit began to be determined from plumage coloration in 1991, we have materials on the age and sex composition of only 1115 birds. Of these, young immature individuals (83.1 ± 1.2%) and females (65.1 ± 1.5%) predominated during migrations in 1991–2016. At the beginning of autumn migration, in the second half of September, mainly young birds migrated, and adults appeared only from October.

Based on ring recoveries, it is possible to calculate the approximate ratio of the age of owls in annual terms, using even individuals whose age at the time of ringing was unknown, since on average more than 80% of the ringed birds were young individuals. Having calculated the proportion of owls found with rings at the age of 1 year or more (1+), 2 years and more (2+), 3 years and more (3+), etc., we thus obtained the age structure (Fig. 3). It turned out that mainly young owls also fell into human hands; they account for up to 65.7% of the number of those found. The longevity record was at least 16 years and 3 months.

Migratory Movements, Wintering Areas, and the Circumstances of Findings of Ringed Owls

The monthly distribution of the number of long-eared owls caught on the Curonian Spit shows (Fig. 4) that the peak of their migration in autumn falls on October and early November. Spring migration is weakly expressed, a small increase in the number of owls occurs in April and May. The number of ring recoveries is more or less evenly distributed throughout the year, with the exception of a decline during the summer months. The periods of ringing owls turned out to be much narrower than the ring return periods.

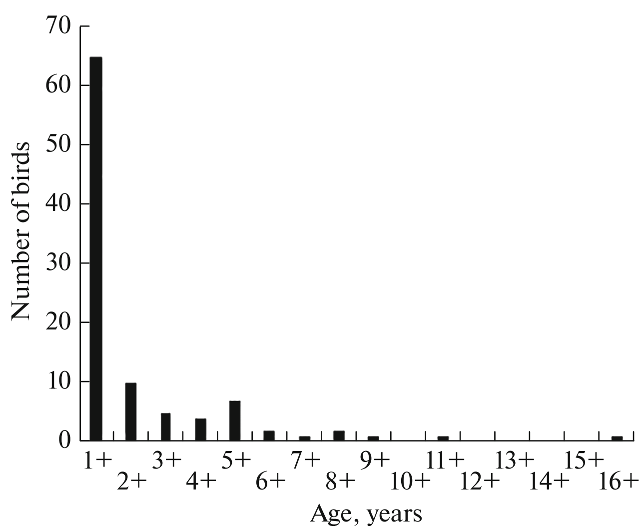

Fig. 3. Approximate ratio of ages in years among the birds that yielded ring recoveries.

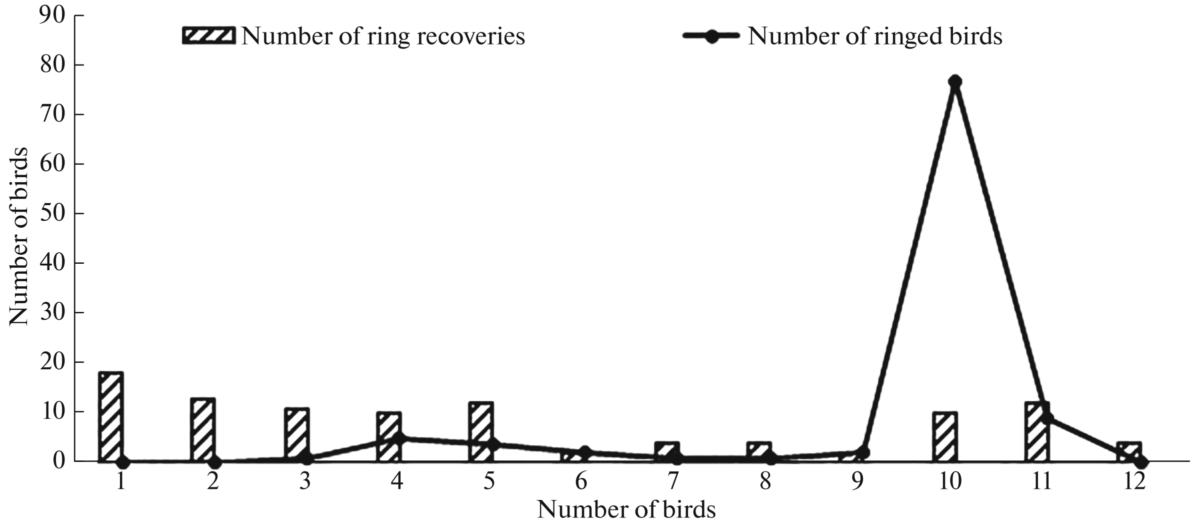

Fig. 4. The number of long-eared owls caught and ringed in different months of the year (curve) and the number of individuals found in different months in the territories of migration and wintering (histogram).

Of all the 102 owls found with our rings, only 16 birds (15.7%) were found alive (of which nine were caught and released and seven were caught, but their fate was not reported). Among the remaining owls, 62 individuals (60.8%) were found dead or dying, including birds killed by predators, as well as the remains of birds with rings; 12 (11.7%) were killed by human beings and 12 (11.7%) were victims of collisions with vehicles.

Of the total number of ring recoveries, some ($n = 45$) belonged to the same season as the ringing season (these are the so-called "direct" recoveries), with a range of flight distances from 54 to 1774 km, while the rest ("indirect" recoveries, $n = 57$) were related to subsequent seasons, with a range from 47 to 1790 km. The average distances of migrations were 820.0 ± 64.2 and 833.9 ± 57.7 km based on direct ring recoveries and indirect ones, respectively; there were no significant differences between them ($\chi^2 = 58.9$, df = 44, n.s.).

The scatter azimuth varied from 22° to 355° (on average 239.5° ± 12.4°) for direct recoveries and from 18° to 322° (on average 211.7° ± 10.1°) for indirect recoveries, without significant differences ($\chi^2 = 1.12$, df = 44, n.s.). Consequently, the average bearing of the points of detecting most owls was to the southwest of the place of our ringing. Nevertheless, some individuals moved both south and northwest, flying even over the ocean.

The location of all the points of finds of ringed long-eared owls is shown in Fig. 5. Their distribution among the countries of Western and Eastern Europe reflects a different degree of concentration on migration routes and wintering areas. The highest numbers of ring recoveries come from Germany (33), Russia (13), Poland (9), Belgium (8), the Netherlands (8), France (7), and Finland (6). The longest flight distance is up to 1774 km. Ring recoveries from the territories located north and east of the Curonian Spit (15 birds) presumably indicate a widespread origin of the populations of birds migrating through the Curonian Spit, namely, from Lithuania, Latvia, Belarus, and Finland, as well as from different areas of Russia—Leningrad, Tver, Ryazan, and Moscow oblasts and Tatarstan. With the supposed return of owls to the breeding grounds by the same route, the angle of their scattering to the breeding grounds can be from 10° to 96°, and the distance can be up to 1790 km.

The nomadic way of life of long-eared owls in the areas of wintering may be evidenced by different lengths of migrations according to the ring recoveries in different months of the year. According to our data, long-eared owls are found in Europe in all months of the year, but they are more often found from October to the end of May. Figure 6 shows the distances from the place of ringing to the points of detection of long-eared owls in different months. From October to March inclusive, these distances gradually increase, on average from 671 to 1027 km. Pairwise comparison of distances (October–November, November–December, etc.) according to their central trend using the nonparametric Wilcoxon test showed no significant differences in all cases, and only a comparison of distances in October with distances in March was at the boundary of the significance of difference (median of 642 and 1087 km, d.f. = 9, $n_x = 78$, $p < 0.05$). The azimuths of the points of direct recoveries in October–November (on average 245°) and January–February (on average 240°) did not differ significantly ($\chi^2 = 3.2$, d.f. = 7, n.s.). Thus, in general, a slight increase in the length of migrations starting from October may also indicate the movements of owls during the winter, but it is impossible to draw a reliable conclusion about

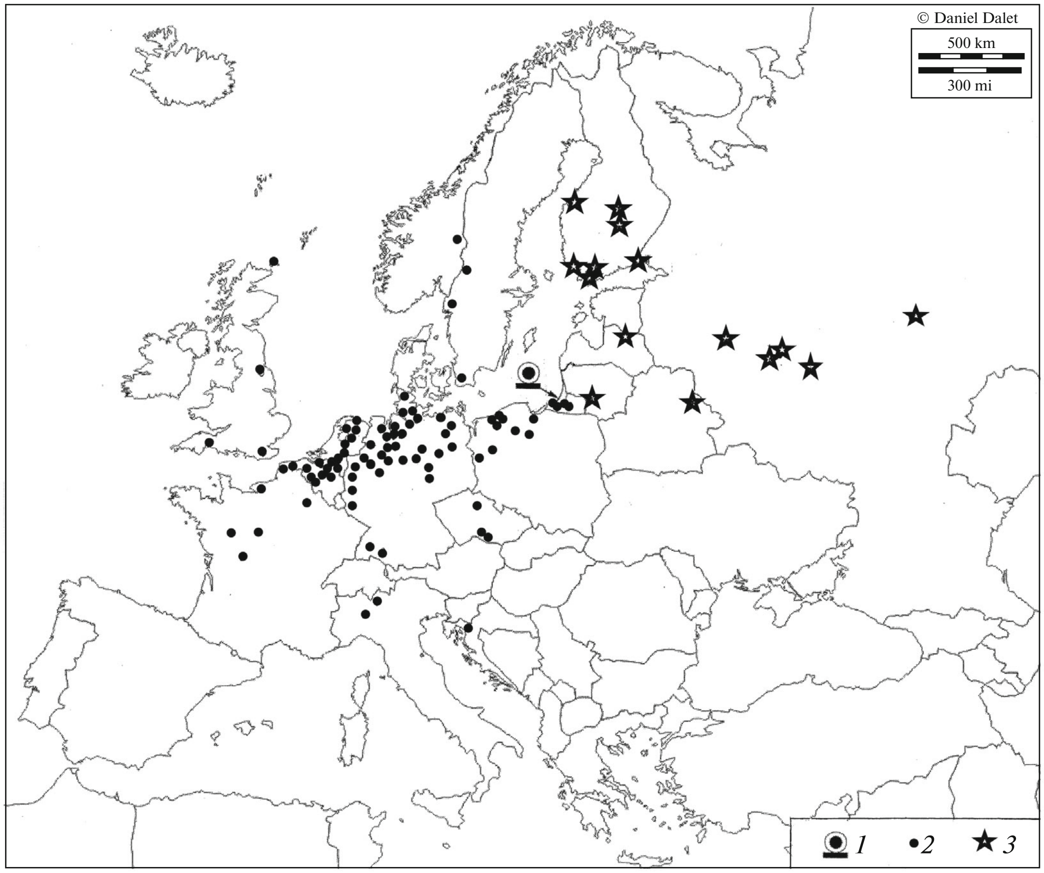

Fig. 5. Distribution of long-eared owls ringed on the Curonian Spit on migratory routes and on wintering areas and breeding areas: (*1*) ringing site, (*2*) detection points on migration routes and wintering areas, and (*3*) detection points on possible nesting sites.

this. In April and May, some owls were still in Western European countries, but not in breeding areas. Whether such staying on the migration routes is related to the age of birds and the timing of their reaching a sexually mature state, or whether this is due to other reasons, remains unknown.

Daily Flight Speed

We managed to determine the reliable speed of movement of long-eared owls along migration routes only in eight birds that were found 7–40 days after ringing. Two of them were ringed during spring migration, and the rest were ringed during autumn. The speed of movement varied from 21.6 to 58.2 km, averaging 36.4 km per day.

DISCUSSION

Comparative Efficiency of Ringing Long-Eared Owls

The results of ringing migratory owls on the Curonian Spit in the form of received ring recoveries amounted to 3% of the number of ringed birds. These results were more successful than the efficiency of ringing small songbirds, which often did not exceed even 1%. Previously, we have already tested this dependence for different bird species and found that, despite the actual decrease in the proportion of returns, in many cases there was no significant correlation between the number of ringed birds and the number of recoveries. Apparently, the weather and other conditions of the year can significantly affect this indicator. The efficiency of ringing long-eared owls until the mid-1990s in different European countries varied from 0.5 to 10.1%, averaging 5.1% (Payevsky and Shapoval, 1998). Today, in Finland, the efficiency of ringing long-eared owls also reaches 5.5%, although, in contrast to our data on ringing migratory birds, more than half of the individuals were ringed there at nestling age (Saurola, 2014). It is known that, since the 1980s, information has appeared in the ornithological literature about a significant decrease in the proportion of ring recoveries of all bird species compared with previous decades. Apparently, the change in people's attitude to the need to report a ringed bird is an important reason for the reduction in the proportion of ring recoveries (Payevsky and Shapoval, 2013).

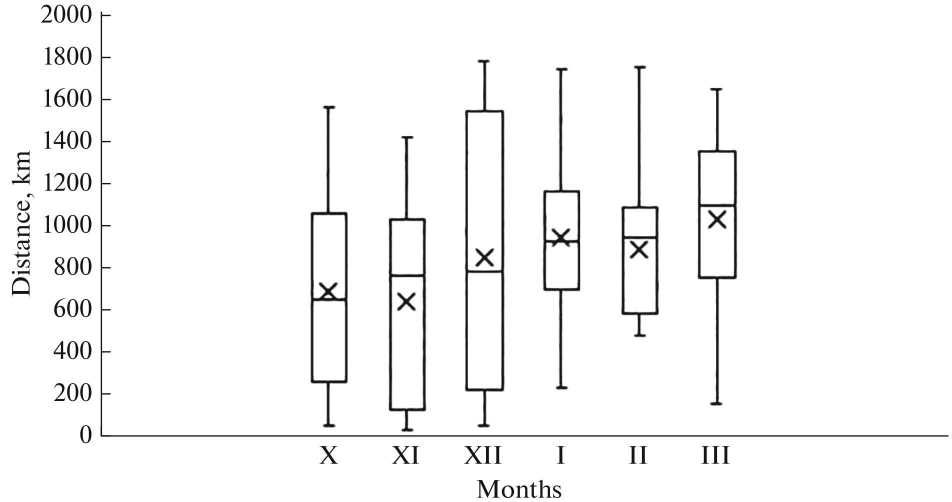

Fig. 6. Distance from the place of ringing on the Curonian Spit to the places where ringed long-eared owls were found in different months, October–March. The vertical lines are the range of values in kilometers, the rectangle contains half of the values, the cross indicates the arithmetic mean, and the horizontal line is the median.

Issues of Cyclicity in the Number of Migrants

Sharp annual fluctuations in the number of long-eared owls caught have inevitably led to questions about the causes of this phenomenon and its relationship to the characteristics of the owl life cycle. Is there a cyclicity in the population sizes of this species? Records of catching long-eared owls in the territories of other parts of the Baltic, from where the birds could come to the Curonian Spit, also testify to the huge year-to-year fluctuations in the number of long-eared owls caught. At the Latvian Pape ringing point, the fluctuation range was from one to 960 individuals (Graubits, 1976; Rute and Baumanis, 1986); at the Polish Bukovo–Kopan point, it was from 8 to 736 (Busse, P. and Busse, W., 2003; Michalonek et al., 2005). Comparison of data from different ringing points shows the lack of synchronism in the dynamics of captures; however, at our and Latvian stations, the period from 1975 to 1979 was characterized by the highest abundance of the long-eared owl, while in Poland such a period was 2000–2002 (Michalonek et al., 2005). In North America, peaks of mass migratory movements of the long-eared owl could indicate both 10- and 3-year abundance cycles. At the same time, the diversity of both directions and distances of movement of owls in Canada and the United States could indicate a nomadic lifestyle due to an unstable food base (Houston, 2005).

It is known that the numbers of long-eared owls and the degree of their territorial mobility depend entirely on the abundance of the main food—voles—which changes abruptly in different years, moreover, asynchronously in different areas. The number of breeding owls and their redistribution during nesting depend significantly on vole abundance, both immediately before the start of breeding and in the previous autumn, and in the years of their absence owls do not start breeding at all (Korpimäki, 1992, 1994; Volkov et al., 2009). Some of the populations of long-eared owls during the peak of vole abundance remain to winter in more northern territories (Korpimäki and Nordahl, 1991; Korpimäki, 1994). Moreover, many cases of winter and autumn–winter nesting have recently been recorded in many places in Europe, from Russia to Italy and the United Kingdom (Morozov and Kontorshchikov, 2008; Noga, 2009; Khrabry and Baibekova, 2015). In general, this species is characterized by very extended dates of egg laying, which occurs in summer even until mid-June (Shapoval, 2013). All this once again confirms that the reproduction of the long-eared owl occurs only if there is a sufficient food base. The abundance in autumn and winter in different regions ranges from several tens to several hundreds of birds according to the results of many studies (Konstantinov et al., 1982; Sharikov et al., 2002). Consequently, the number of migrating owls can also undergo various large-scale changes. This is exactly what the data of our long-term capture on the Curonian Spit reflect; nevertheless, there is no strict cyclicity in these fluctuations.

Some researchers, in both Europe and North America, believe that the number of long-eared owl populations has been declining in recent decades (Houston, 2005; Noskov and Lapshin, 2016). However, data on the breeding success of this species in different regions do not confirm this fact. Interannual fluctuations in the number of owls in Finland in 1986–2015 were very large, but, nevertheless, the breeding success remained close to the long-term average. The average number of nestlings per successful nest was 2.94 (Björklund et al., 2015). Almost the same (3.0) number of nestlings per successful nest was also noted in another region of Europe, in Belarus (Ivanovskii, 2015).

Ratio of Age and Sex Groups among Migratory Long-Eared Owls

The significant predominance of young birds (83%) and females (65%) among the migrants that we caught may, presumably, indicate a reduced migratory stimulus in old males, although we have no supporting data. On the Baltic coast of Poland in 1996–2003, young birds also predominated among 2044 captured migratory long-eared owls, accounting for 89.4 ± 0.7% (Michalonek et al., 2005). Despite the variations in indicators in different years, these very similar values of the average shares in our country and in Poland (83 and 89%) indicate, first, the reliability of the information received by ornithologists on the age composition of migratory owls and, second, the possible common territorial sources of migratory populations for the Eastern and Southern Baltic.

It is known that the sequence of autumn migration of different age and sex groups of birds has its own characteristics. According to various studies, young individuals of both sexes, as well as females of different ages, are the first to fly away in autumn in a number of bird species and the proportion of males and adult birds gradually increases towards the end of the migration (Payevsky, 1985). As for the long-eared owl, according to our data, only young birds migrated at the very beginning of the migration, in the second half of September, and adults appeared from the first days of October. However, according to the results of capture in Poland, the opposite sequence was noted: adult owls migrated a little earlier than young ones, 1–16 days earlier in different years (Michalonek et al., 2005).

According to the data of recoveries of our rings, it turned out that mainly young owls also fell into human hands, accounting for up to 65.7% of all found birds. Very similar data on the ratio of different ages based on ring recoveries and the results of ringing in Finland are also given. Owls of the first year of life accounted for 57.8% there (Saurola, 2014). As for the maximum longevity of this bird species, the figures from different countries and continents are also very similar: 16 years and 3 months in Russia, 17 years and 8 months in Finland (Saurola, 2014), and 15 years and 8 months in North America (Houston, 2005). According to the survey on the maximum longevity of birds, the average value for all bird species from the order of owls was 15 years (Wasser and Sherman, 2010).

Causes of Mortality in Long-Eared Owls; Their Migratory Movements and Main Wintering Grounds

Our ring recoveries have been found to be more or less evenly distributed across the months throughout the year, with the exception of an almost complete decline during the summer months. Approximately the same distribution of these indicators by months of the year exists according to published data from Finland (Saurola, 2014). The difference from the indicators from Finland was that, according to our data, only about 16% of birds among ring recoveries were found alive, while, according to the materials from Finland, 29% of 756 birds that gave ring recoveries were found alive (Saurola, 2014). Of all the various causes of death of ringed owls (direct killing by human beings, collision with vehicles, killing by other birds of prey, etc.), the largest proportion, 56%, remains unknown, since these birds with our rings were found dead or dying.

Reports of ringed birds are widely used to map migratory routes and wintering areas. However, in some cases, there are some doubts about the correctness of the picture of the distribution of migrants obtained in this way. Doubts arise from the obvious circumstance that the number of ring recoveries depends on the density of human settlements and cultural level of reporters. One of the main factors distorting the data obtained is the concentration of hunters and birders in some places in Europe (Payevsky, 1973; Busse, 2001). However, this circumstance may not be so important for owls, which, unlike many other birds, are nocturnal.

The distribution of migrating owls across Europe, which is shown on the map (Fig. 5), undoubtedly indicates that the part of the territory of Europe that is limited by latitude 50°–54° N and longitude 1°–16° E is the main place where long-eared owls migrating through the Curonian Spit, i.e., where birds from the Baltic, Leningrad, Tver, Moscow and Ryazan oblasts aspire to go. They winter mainly in northern Germany, the Netherlands, and Belgium. However, individual birds are found over a vast territory, from Italy to Norway. The wintering grounds of long-eared owls from Finland also occupy regions that are very far from their breeding grounds, from Norway and the British Isles to Belarus and Ukraine, although the median of their wintering grounds is in Denmark (Saurola, 2014).

The Speed of Flights according to Ring Returns

The study of the speed of migratory-bird movements is one of the necessary aspects of detailed studies of their seasonal flights. More or less extended migrations typically include several flight cycles, stops and starts for the next flights. The behavior of migrants during the flight and at stopovers is determined by their species-specific foraging behavior and weather and habitat conditions. The average speed of movement of owls obtained by us, which is equal to 36.4 km per day, is quite significant in comparison with other bird species. For most bird species, the values of the average daily movement speed range from 20 to 100 km (Payevsky, 2012). Of course, compared with ringing, the data obtained using telemetry, primarily satellite, in some cases fundamentally change traditional ideas about both migration routes and migration speed. At the same time, the reliability of such data nevertheless depends on the accepted condition that the attachment of a transmitter to a bird, like the attachment of a ring, does not change its migratory behavior.

CONCLUSIONS

Summarizing all the data on ringing long-eared owls over the course of six decades has made it possible to identify a number of features of their migratory movements. First, there is a very pronounced annual instability of the mass migration, which is also observed in other habitats of the species and is associated with the cyclical abundance of the main food object—mouselike rodents, primarily voles. Second, despite the main southwestern direction of autumn movements after migration over the Eastern Baltic and the predominant wintering in Germany, Belgium, the Netherlands, at latitudes of 50°–54°N, there is a very wide distribution of individual migratory birds over Europe, from Italy and Croatia to Sweden, Norway, and the Orkney Islands in Scotland. Third, huge distances, which reach more than 2000–3000 km according to calculations, are overcome by some birds flying from breeding places to wintering grounds. Fourth, the age composition of migrating owls is characterized by the predominance of young birds both according to our data and according to data from different ringing sites in Europe and North America, as well as a similar maximum longevity of individual birds, which is from 15 to almost 18 years.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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