ISSN 1067-4136, Russian Journal of Ecology, 2017, Vol. 48, No. 3, pp. 256–261. © Pleiades Publishing, Ltd., 2017.
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Dynamics of Phenotypic Traits and Intrapopulation Processes in Great Tit (*Parus major* L.) Populations of the Middle Ural

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Received March 24, 2016

Abstract—Variability of the length of the white area on the outermost quill feathers of the great tit from two cities in the Middle Ural has been investigated. Dynamics of the average length of the white area in the birds from the city of Asbest reproduced the dynamics observed in the city of Yekaterinburg with a one-year lag in the females and a two-year lag in the males. Phenotypic changes in the great tit population did not occur simultaneously in the whole population, but rather moved along the living range with a certain velocity (50–60 km/year for the females and 25–30 km/year for the males). The results obtained are discussed in view of the concepts of population biology.

Keywords: great tit, variability, population structure

DOI: 10.1134/S1067413617030067

INTRODUCTION

Population biology is currently among the most important research areas in ecology. This field of research encompasses the identification of natural populations and boundaries thereof, investigation of population structure and functional features of the populations under specific ecological conditions, and elucidation of the mechanisms that underlie the formation and maintenance of the population structure of a species.

Identification of natural populations is a complex task, and there are few examples of groups reliably identified as populations [1]. The detection of populations is usually feasible in the case of species characterized by low mobility of the individuals or in the case of groups separated by unsurmountable physical obstacles (for instance, in the case of island populations). Research on bird populations is especially difficult due to the high mobility of birds, their capacity for migration over long distances, and the ability to surmount virtually any physical obstacles [2].

Analysis of the variability of morphological traits, including the color patterns, is one of the approaches that can be potentially useful in the search for a solution of this problem. A.S. Serebrovskii [3] was the first to demonstrate the possibility of identifying natural bird groups of different levels, from population to smaller groups, according to the distinctive features of the color pattern [4–8].

The great tit (*Parus major*) is considered the most suitable object for studies of this type. The species is "sedentary" and the migration of resettling individuals is restricted (that is, the migration distances range from tens to hundreds of kilometers). The restricted character of migratory activity of the great tit is apparent from the polytypic structure of the species as well. The great tit inhabits the major part of Eurasia and occurs as up to 30 forms and subspecies. Certain researchers in the field of systematics consider *Parus major* a supraspecies and subdivide it into 3–4 species [9].

Variability of color traits, including the depigmentation of the quill feathers, was reported for the great tit [7, 8, 10, 11]. The character of depigmentation of the quill feathers, and the length of the white area of the internal vexillum of the outermost quill feathers in particular, shows considerable geographic variability in the great tit and is therefore used by researchers in the field of systematics for the identification of subspecies and local geographic forms.

The present study reports the results of 14 years of monitoring of the length of the white area of the internal vexillum of the outermost quill feathers of the great tit at two geographically distant sites in the Sverdlovsk oblast. The aim of the study consisted in comparative analysis of the dynamics of this trait, identification of

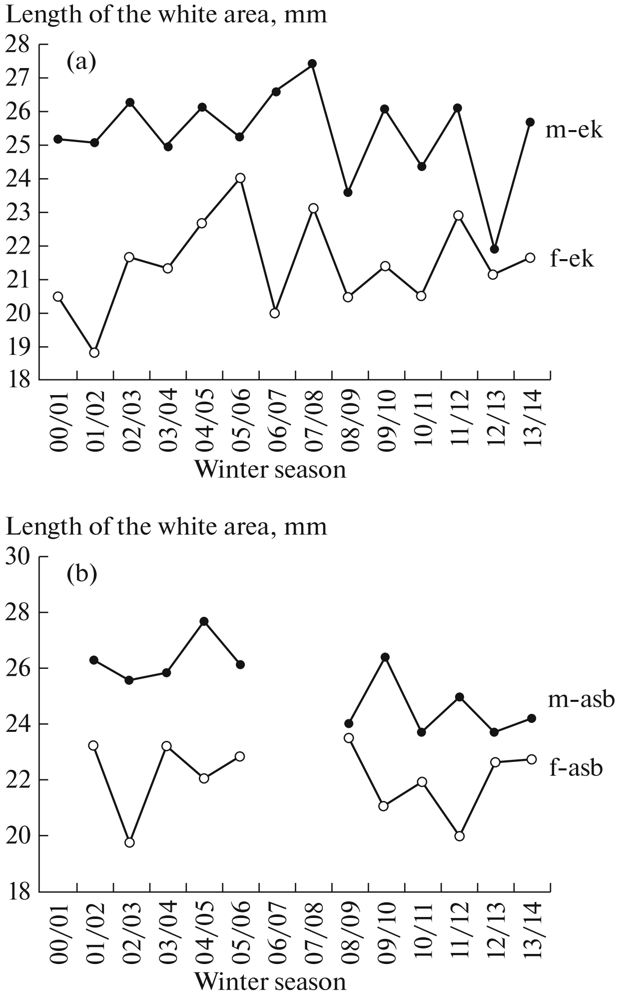

Fig. 1. Dynamics of the average size of the white area of the sixth quill feather in great tit individuals from the cities of Yekaterinburg (a) and Asbest (b) in the winter period: m-ek—males, Yekaterinburg; f-ek—females, Yekaterinburg; m-asb—males, Asbest; f-asb—females, Asbest.

phenotypic differences between the bird groups under investigation, and assignment of these groups to a single great tit population or different populations. Thus, the study was performed within the framework of the chronogeographical approach to the analysis of population structure put forward and developed by A.G. Vasil'ev [12, 13].

MATERIALS AND METHODS

The material was collected in the winter period during the years 2000–2014 in the city of Yekaterinburg and in the years 2001–2006 and 2008–2014 (that is, with a small break) in the city of Asbest (Sverdlovsk oblast). The straight-line distance between the capture sites was approximately 60 km. Great tits were captured at feeders after the formation of a permanent snow cover and relative stabilization of the wintering bird population (between November and January). The birds captured were weighed and measured according to the standard procedures, and the length of the white area of the internal vexillum of the outermost quill feathers was measured in all birds. All measurements were performed in vivo, and the birds were released after measurement and ringing with aluminum rings. The total number of birds captured in Yekaterinburg was 799 (428 males and 371 female), and that of the birds captured in Asbest was 926 (493 males and 433 females). According to the recommendations given by B.L. Astaurov [14], the side of the body was taken into account as a measurement parameter during the investigation of bilateral structures. Therefore, the length of the white area was measured both on the left and on the right, and all calculations were performed for the entire set of body sides investigated. The birds were not divided into groups of young and mature individuals, since the relative numbers of individuals of different ages changed non-uniformly from year to year and the young birds predominated considerably in almost all samples.

Microsoft Excel 2003 and Statistica v. 6.0 (StatSoft, Inc., 1984–2001) software were used for statistical processing of the data. The average values of the length of the white area in males and females were calculated for each season, and multiannual series for the average values were constructed and compared using Pearson's correlation coefficient.

RESULTS AND DISCUSSION

Variability of the average length of the white area in male and female birds from the Middle Ural is characterized by the values in Table 1. A clear sexual dimorphism in the manifestation of the trait was apparent, since the values for the males were always higher than the values for the females. There were no significant differences between the cities with regard to the average size values and the ranges of variation of the length of the white area. Observations performed over many years revealed considerable variability of the average values of the length of the white area of the sixth quill feather both in females and in males at both sites investigated (Fig. 1). A two-year cycle sometimes transformed into the three-year cycle was clearly apparent from the pattern of variability. No trend was revealed in the changes of the length of the white area during the study period, although the values for the male birds from Asbest might have decreased to a certain extent. One should also emphasize the non-synchronized character of the changes of this parameter in Yekaterinburg and Asbest. Interestingly, the pattern of trait dynamics in male and female birds of Asbest showed clear opposite trends (Fig. 1b).

However, detailed analysis of the dynamics of the average length of the white area revealed interesting regularities. Firstly, the dynamics of this trait in the females from Asbest was virtually identical to that in the females from Yekaterinburg, except for a one-year

Length of the white area of the sixth quill feather of great tit individuals from Yekaterinburg and Asbest (*n* is the number of sides investigated)

Winter season, years	Males			Females		
	n	*M* ± *m*	lim	*n*	*M* ± *m*	lim
Yekaterinburg						
2000/01	33	25.18 ± 1.19	8–41	18	20.50 ± 2.17	0–30
2001/02	54	25.07 ± 1.14	7–40	37	18.78 ± 1.58	3–33
2002/03	84	26.26 ± 0.80	6–43	47	21.67 ± 1.16	5–35
2003/04	46	24.94 ± 1.26	5–40	37	21.30 ± 0.93	7–30
2004/05	48	26.13 ± 1.23	4–40	40	22.66 ± 0.97	5–32
2005/06	50	25.24 ± 1.01	5–39	40	24.02 ± 1.01	5–34
2006/07	50	26.58 ± 1.18	10–41	55	19.95 ± 1.26	4–37
2007/08	54	27.44 ± 0.95	5–37	63	23.15 ± 0.83	4–32
2008/09	59	23.63 ± 1.06	6–36	55	20.50 ± 0.90	4–33
2009/10	64	26.08 ± 0.69	11–40	52	21.39 ± 1.11	5–36
2010/11	94	24.38 ± 0.80	6–41	68	20.46 ± 0.95	4–34
2011/12	71	26.11 ± 0.85	5–39	72	22.90 ± 0.85	3–36
2012/13	74	21.92 ± 1.03	6–47	66	21.15 ± 0.95	4–37
2013/14	70	25.69 ± 1.08	3–41	92	21.69 ± 0.74	3–36
Asbest						
2000/01						
2001/02	88	26.28 ± 0.75	11–43	98	23.19 ± 0.69	5–39
2002/03	133	25.58 ± 0.63	6–41	130	19.74 ± 0.68	1–40
2003/04	114	25.81 ± 0.68	7–38	123	23.22 ± 0.71	5–40
2004/05	68	27.66 ± 0.89	10–43	62	22.05 ± 0.91	5–37
2005/06	77	26.17 ± 0.81	5–40	92	22.86 ± 0.69	6–35
2006/07	–	–	–	–	–	–
2007/08	–	–	–	–	–	–
2008/09	74	24.04 ± 0.80	10–37	60	23.52 ± 1.10	3–37
2009/10	59	26.45 ± 0.87	6–37	41	21.05 ± 1.16	5–36
2010/11	90	23.64 ± 0.76	4–37	63	21.93 ± 0.87	4–34
2011/12	128	24.96 ± 0.67	2–43	101	20.00 ± 0.77	5–35
2012/13	84	23.70 ± 0.84	3–44	58	22.66 ± 1.08	2–32
2013/14	67	24.19 ± 0.90	5–48	29	22.77 ± 1.40	4–35

lag (Fig. 2). The average values were very close as well. In other words, similar changes of the average size of the white area were first observed in Yekaterinburg and one year later in Asbest. The correlation coefficient calculated for the series without shifting was $r = -0.32$ ($p = 0.332$), whereas the correlation coefficient for the values shifted by one year was $r = 0.75$ ($p = 0.007$). Firstly, this result means that the great tits of Yekaterinburg and Asbest are very likely to belong to the same population that undergoes the same processes (such as the phenotypic changes analyzed in the present study). Secondly, phenotypic changes do not occur at the same time in the entire population, but rather spread over the living range (from west to east in the case of the population investigated in the present study) at a velocity of approximately 50–60 km/year (the approximate straight-line distance between the cities). The putative locus where these changes started could not be identified using the material collected, and the actual direction of the spreading of the changes along the living range could not be determined either, but we can confidently state that the changes took place. The mechanism that underlies the spreading of these changes over the living range is probably related to migration of the birds in the direction named above.

The annual cycle of the great tit is known to include three periods of migration. Summer migration that

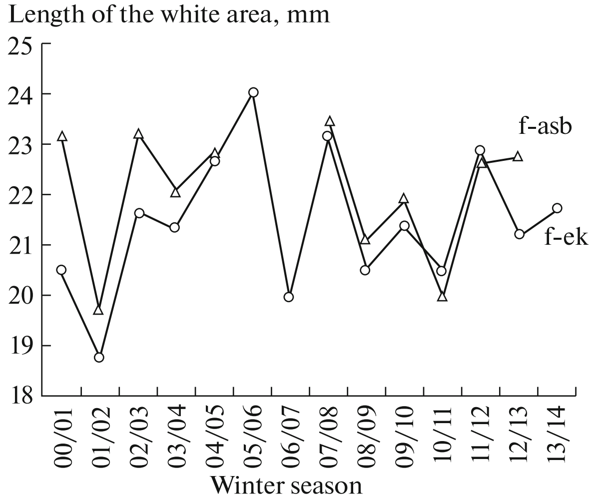

Fig. 2. Dynamics of the average size of the white area in great tit females from Yekaterinburg and Asbest in the winter period. The range for Asbest is shifted backwards by one year. Symbols same as in Fig. 1.

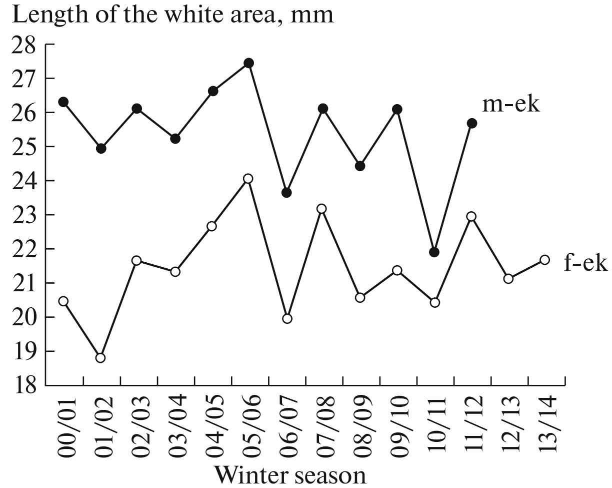

Fig. 3. Dynamics of the average size of the white area in great tit males and females from Yekaterinburg in the winter period. The range for males is shifted backwards by two years. Symbols same as in Fig. 1.

involves young birds only is considered an essential ontogenetic phase similar to those observed in other "sedentary" species. Postfledging dispersal of the young birds is of genetic significance, since it ensures the prevention of inbreeding within the populations. The autumn migrations usually have mass proportions and involve 10–20% of the mature birds, in addition to the young birds [15, 16]. The spring migration mostly involves young birds [17]. The birds form a connection with the territory after the first breeding and usually retain this connection during the entire life [15]. Thus, intra- and interpopulation exchange in great tits is largely due to the activity of young birds. Mature birds mostly migrate between wintering and nesting areas during the entire lifetime.

We assume that the character of migration from Yekaterinburg towards Asbest remained unchanged at least during the entire observation period (14 years). Importantly, great tits ringed in Yekaterinburg were never encountered in Asbest (and vice versa). The scale of ringing during the years of study was not large enough to allow for unambiguous conclusions; however, this finding can be regarded as additional proof of the leading role of young birds in the spreading of phenotypic changes. The wintering birds apparently do not migrate over long distances any more.

In general, the facts observed point at certain long-term processes accompanied by considerable phenotypic changes in the great tit populations. Research on these changes is of great theoretical interest, since the changes are manifested as certain phenotypic waves that move along the living range of the population similarly to ripples on water. Similar processes of the spreading of phenotypic changes that start in a local habitat and gradually expand to large areas were reported previously [18 and others].

Dynamics of the average length of the white area in females and males from Yekaterinburg is illustrated in Fig. 3. The dynamics of this trait in male birds apparently reproduced the dynamics observed in females, except for a two-year lag ($r = 0.64$, $p = 0.025$). Thus, the phenotypic changes first occurred in the females, and the same changes in the males occurred with a two-year delay. The males apparently were the offspring of the females that were the first to exhibit the changes, and thus inheritance of the trait under investigation can be assumed, but the exact degree of relationship (first- or second-generation offspring) and the character of inheritance of the trait cannot be inferred from the material collected for the present study.

Importantly, a regularity of this type was not detected in the bird population from Asbest: the dynamics characteristic of the males from Asbest was largely similar to that observed in the males from Yekaterinburg, although a two-year lag was observed (Fig. 4). The correlation coefficient was not very high in this case ($r = 0.43$, $p = 0.210$) due to a smaller number of observation points than in the previous cases, but the similarity of dynamics illustrated by the graph appears undeniable to us.

Therefore, phenotypic changes in the males were first recorded in Yekaterinburg and later in Asbest, and this confirms the unity of the group of birds investigated. However, the time lag between the changes at different sites amounted to 2 years, whereas the lag in the females was only one year long; thus, the migration of males was twice slower.

Interestingly, the clear correlation between the patterns of change of the trait in birds from the cities of

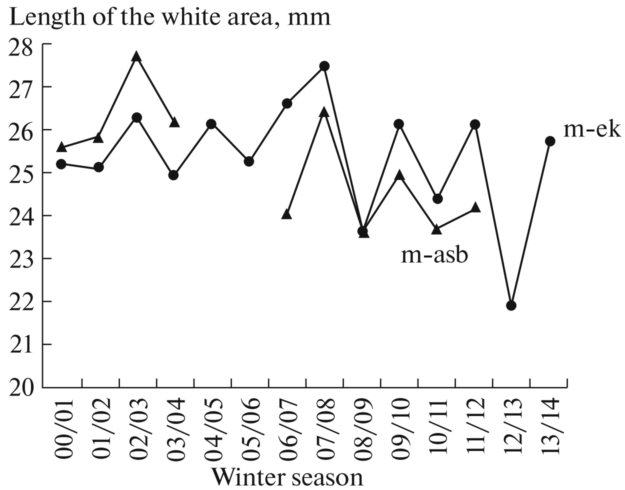

Fig. 4. Dynamics of the average size of the white areas in great tit males from Yekaterinburg and Asbest in the winter period. The range for Asbest is shifted backwards by two years. Symbols same as in Fig. 1.

Yekaterinburg and Asbest pointed at a decisive contribution of great tits of Yekaterinburg. One can assume that the size of the group of resident birds in the environs of the city of Asbest is much smaller than the size of the migrant bird population. This can be due to considerably larger numbers of wintering birds in the environs of the city of Yekaterinburg, a higher degree of survival, and the subsequent more efficient breeding in these birds.

Recent studies [10, 19] showed that the large cities in the east of Russia (that is, in Ural and Siberia) became wintering sites and, at the same time, population centers of the species. An increase of the degree of sedentariness, strong attachment to wintering and breeding sites, and the reduction of migration distance were observed in the great tit populations [10]. Interestingly, the survival rate of young birds amounted to 85% [19] in large cities where feeders were available, although the level of mortality in this group of birds is usually presumed to be high. This apparently leads to considerable local growth of population size and density.

A certain demographic pressure directed towards periphery arises, that is, the "outflow" of young birds along the population density gradient takes place. However, one cannot rule out the existence of certain regional migratory processes that incorporate the pattern observed by us as a small fragment. In this case, the great tits from Asbest would be involved in these processes as well, and the offspring of these birds would accordingly migrate even further. The detection of these processes in great tit populations apparently is a promising topic for further research.

The leading role of the female birds from Yekaterinburg in these processes deserves a special mention. All phenotypic changes started (or at least, were first detected) in this local group of birds, and then expanded to the males from Yekaterinburg and to all birds from Asbest (the characteristic time of the spreading of changes differed for the different target groups). At this, the contribution of other groups of birds appeared negligible: the erosion of phenotypes was very slight, if present at all, and thus had virtually no masking effect on the major pattern of similarity of phenotypic dynamics. This nontrivial result requires further investigation and interpretation.

A.V. Yablokov used the analysis of his own data and published studies to put forward a novel concept of the radius of reproductive activity (the distance between the birth site and the reproduction site for 95% of individuals of a specific generation) [1]. This is an integral parameter that reflects a number of fundamental genetic and ecological features of the processes in a population. Our results showed that the radius of reproductive activity could be different in males and females of the great tit: the value for the females was not less than 60 km, whereas that for the males was approximately twice less. However, one should remember that this parameter is not necessarily the same for different parts of the population and for different directions. For instance, southward migration was shown to predominate among the directions of autumn migration of the great tit [15].

Thus, many years of research on the dynamics of a phenotypic trait in the great tit revealed large-scale processes in the natural populations, such as the directions and vectors of the migration and the velocity of spreading of the phenotypic changes (**phenotypic waves**). We believe that now the assessment of the information flow between different parts of the population has become possible in principle, and this is of great importance for research on the microevolution processes. In general, research on phenotypic variability opens ample opportunities for the investigation of natural populations, and an appropriate research setup provides answers for a wide range of extremely complex problems of population ecology, regardless of the relative simplicity of the methods used. Moreover, wildlife objects that were previously not amenable for investigation due to specific biological features can now be involved in the studies described above.

REFERENCES

1. Yablokov, A.V., *Populyatsionnaya biologiya* (Population Biology), Moscow: Vysshaya Shkola, 1987.
2. Danilov, N.N., Population structure of species in birds, *Ekologiya,* 1983, no. 3, pp. 12–17.
3. Serebrovskii, A.S., Gene geography and gene pool of farm animals in the Soviet Union, *Nauch. Slovo,* 1928, no. 9, pp. 3–22.
4. Beregovoi, V.N., The problem of subspecies and populations of polymorphic species, *Zh. Obshch. Biol.,* 1967, vol. 28, no. 1, pp. 50–63.

5. Volchanetskii, I.B., On the study of geograpgic variation in bird plumage pattern and color, in *Problemy evolyutsii* (Problems of Evolution), vol. 2, Novosibirsk: Nauka, 1972, pp. 198–211.
6. Koryakin, A.S., Krasnov, Yu.V., Tatarinkova, I.P., and Shklyarevich, F.I., On the population structure of common eider, Somateria mollissima, in the Northwestern Soviet Union, *Zool. Zh.,* 1982, vol. 61, no. 7, pp. 1107–1110.
7. Likhatskii, Yu.P., Evaluation of phenetic relationships between spatial groups of birds by elements of the color pattern of quill feathers (the example of *Parus major*), Ekologiya, 1986, no. 6, pp. 125–131.
8. Likhatskii, Yu.P., Experience in the phenetic study of birds (the example of some passerines), in *Fenetika prirodnykh populyatsii* (Phenetics of Natural Populations), Moscow: Nauka, 1988, pp. 132–140.
9. Kartashov, N.N., *Sistematika ptits* (Bird Systematics), Moscow: Vysshaya Shkola, 1974.
10. Gashkov, S.I., The biology of the great tit, *Parus major* L., in the southern taiga of Western Siberia, Extended Abstract of Cand. Sci. (Biol.) Dissertation, Tomsk, 2007.
11. Tikhomirova, A.V., Comparative characterization of phenetic characters of great tit populations from differentb regiojns of Moscow, *Aktual'nye problemy izucheniya i okhrany ptits Vostochnoi Evropy i Severnoi Azii: Mat-ly XI ornitol. konf.* (Current Problems of Bird Study and Conservation in Eastern Europe and Northern Asia: Proc. XI Ornithol. Conf.), Kazan: Matbugat Iorty, 2001, pp. 592–593.
12. Vasil'ev, A.G., *Epigeneticheskie osnovy fenetiki: na puti k populyatsionnoi meronomii* (Epigenetic Bases of Phenetics: On the Way to Population Meronomy), Yekaterinburg: Akademkniga, 2005.
13. Vasil'ev, A.G., Vasil'eva, I.A., and Bol'shakov, V.N., *Evolyutsionno-ekologicheskii analiz ustoichivosti populyatsionnoi struktury vida (khrono-geograficheskii podkhod)* (Evolutionary Ecological Analysis of Stability in the Population Structure of Species: A Chronogeographic Approach), Yekaterinburg: Yekaterinburg, 2000.
14. Astaurov, B.L., *Nasledstvennost' i razvitie* (Heredity and Development), Moscow: Nauka, 1974.
15. Noskov, G.A. and Smirnov, O.P., Some features of territorial behavior and migrations of the great tit, Parus major, and their adaptive significance, *Materialy 9-i Pribaltiiskoi ornitol. konf.* (Proc. 9th Baltic Ornithol. Conf.), Vilnius, 1976, pp. 191–194.
16. Poluda, A.M., Features of migratory movements of the great tit, *Parus major,* in the region of Kiev Reservoir, *Vestn. Zool.,* 2010, vol. 44, no. 2, pp. 125–136.
17. Golovan', V.I., On spring migration of the great tit, *Parus major,* in the southeastern Ladoga region, *2-ya Vsesoyuznaya konf. po migratsiyam ptits: Tez. soobshch.* (Abstr. 2nd All-Union Conf. in Bird Migrations), Alma-Ata, 1978, vol. 2, pp. 39–40.
18. Mayr, E., *Animal Species and Evolution,* New York: Harvard Univ. Press, 1963. Translated under the title *Zoologicheskii vid i evolyutsiya,* Moscow: Mir, 1968.
19. Gashkov, S.I., Assessment of survival and site tenacity in the Tomsk population of great tit (*Parus major* L.) in the winter period of settled life and during prenuptial migration, *Energetika i godovye tsikly ptits: Mat-ly konf. pamyati V.R. Dol'nika* (Energetics and Annual Cycles of Birds: Proc. Conf. in Memory of V.R. Dolnik), Moscow: KMK, 2015, pp. 98–108.

Translated by S. Semenova