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ECOLOGY

Features of the Annual Cycle of the Life and Ecology of the Arctic Warbler (*Philloscopus borealis* Blas.) from Northwestern Siberia in Comparison with the Willow Warbler (*P. trochilus* L.)

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Abstract—This paper considers the features of the ecology and annual cycle of the arctic warbler in the northern part of Western Siberia, which migrates to wintering places to the southeast in Indo-China, in comparison with the ecology of the willow warbler, which migrates to the southwest to Africa. The influence of the length of the migratory path and the ecological conditions of flight on the nesting ecology of the arctic warbler and the possibilities of advancement of the species to the tundra area of the Yamal Peninsula is analyzed.

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INTRODUCTION

The artic warbler belongs to the inhabitants of the middle taiga, northern taiga, and forest tundra of Eurasia covering an area from Scandinavia to Chukotka, Alaska, and Japan. The area of its highest breeding density is in the taiga zone of Western and Central Siberia (Yudkin, 2009). In 1909, it was first discovered in Finland (Formozov, 1964), where its density is currently low, but stable; in Sweden and Norway, it is not abundant (Atlas, 2003). In the northern taiga of the European part of Russia, it leads in abundance (Ravkin E.S and Ravkin Yu.S., 2005), and on the eastern slope of the Subpolar Urals, it is abundant (Shutov, 1990). In the Ob forest–tundra, the artic warbler penetrated up to the Arctic Circle in the early 20th century (Deryugin, 1898); however, in the Shchuchya River valley it was not found in 1913 by Shukhov (1915) or in 1937–1941 by Kucheruk, Dunaeva, and Osmolovskaya (Kucheruk et al., 1975). At present, it is common in the Lower Ob Region and in the Southern Yamal Peninsula and has penetrated into the Middle Yamal to 69°N (Danilov et al., 1984). Artic warblers winter in Southeast Asia.

In addition to the artic warbler in the Lower Ob Region and in the Yamal, the willow warbler *Phylloscopus trochilus* L. that migrates to Africa over a distance of 5000–6000 km is common on the nesting grounds. The ecology of the willow warbler in our region has been fairly completely studied and described (Danilov et al., 1984; Ryzhanovskiy, 2014). Since the ecology of the arctic warbler and willow warbler was studied simultaneously, the species can be compared in a number of features.

The goal of this work is to describe the ecology and parameters of the annual cycle of the arctic warbler from Western Siberia according to a plan that is common for the willow warbler (Ryzhanovskiy, 2014), to identify the ecological differences between these warbler species, to discuss the influence of the length of the migratory route and the conditions of flight on these differences, to discuss the possibilities of advancement of the artic warbler to the tundra zone.

MATERIALS AND METHODS

The field materials were collected in 1976–1977 in the Polar Urals in the valley of the Sob River (Krasnyi Kamen railway station, 66°40′ N, 66°30′ E) and in 1978–1989 in the valley of the Lower Ob (66°40′ N, 66°50′ E) in the vicinity of the city of Labytnanga (“Oktyabrskii” station). We also worked in the forest islands along the Shchuchya, Khadytayakha, and Yadayakhodayakha rivers in Southern Yamal, where we conducted route surveys and searched for nests. However, the main materials were collected at the “Oktyabrskii” station. In the mixed forest area along the left bedrock bank of the Ob River with an area of 22 ha, we mapped pairs in 1978–1982, and over an area of 38 ha in 2002–2004, we searched for and controlled nests (n = 59), ringed fledglings with aluminum and colored rings, and observed their movements. The last studies were conducted together with Shutov in 1981 (Shutov, 1988).

Some of the information on the ecology was obtained by capturing passerines with mist nets and a trap of the “fishing” type. Nets with a total length of 70–250 m stood from late May to mid-September in

1978–1982, a trap with a southward-oriented entry stood from late May to June in 1979–1978 and 1985–1991, and a trap with a northward-oriented entry was used in 1979–1981. In 2001–2015, artic warblers were periodically caught with nets with a total length of 30–60 m in July–August. Birds were ringed. The body weight, fatness, and age were determined, and the plumage was described by the methods of Noskov and Rymkevich (Noskov and Rymkevich, 1977). The state of plumage of artic warblers was described in detail in 1976–1980, and in subsequent years the plumage was described according to the shortened program. For all the years of regular catches, >1000 young and adult willow warblers were ringed. Three chicks were raised from 10 days of age and caged until autumn.

For the purpose of caging, young ($n = 6$) and adult ($n = 16$) artic warblers were caught in 2010 and 2012 in late July and early August at the "Oktyabrskii" station, were transferred to a cage diet (pupae of the red ant
1 and larvae of the mealworm, chicken egg, cottage cheese, carrots, and multivitamins) and transported to the Middle Urals. The birds lived here from August to early November when the length of the day decreased naturally, then in November–February when the day length was constant (photoperiod 11S:13D), and in March–June when the length of the day naturally increased. Willow warblers proved to be the most capricious among northern insectivores that the author caged (12 species). Having got accustomed to one food, they could refuse another and die. For this reason, a part of the birds survived until spring–summer; at present, two males are alive, their age is 4+. To control the molting process, the plumage was colored with rhodamine alcohol solution.

RESULTS OF STUDY

Spatial, Biotopic Distribution, and Density of Nesting

Currently, in the Lower Ob Region, the area of continuous spread of the artic warbler passes along the northern boundary of the taiga zone, approximately along the 65th parallel. In the forest–tundra zone, the range acquires the form of streams and islands occupied with tall shrubs. In the Yamal, such shrubs penetrate up to the 70th parallel, but the northernmost place of recording willow warbler pairs is 68°50′ N, the valleys of the Yuribei and Nurmayakha rivers, and the Yuribei–Nurmayakha interfluve (Danilov et al., 1984).

When choosing a nesting site in the forest–tundra, birds prefer a mixed forest with undergrowth and moss cover along the slopes of river valleys. At the "Oktyabrskii" station, the highest density of pairs was found in the area of a spruce–birch mixed-herb forest, the lowest density was recorded in a floodplain willow–birch forest, and the middle one was recorded in an alder mixed-grass forest. Among the sparse larch forests of the upland, artic warblers choose areas with an increased density of trees and shrubs. In the mountains of the Polar Urals, the species rises to the limits of growth of individual willow clumps (Golovatin and Paskhal'nyi, 2005).

In the taiga of the Ob–Pur interfluve (Vartapetov, 1998), the artic warbler density was 19–48 individuals/km^2. The artic warbler density was significantly higher in the Lower Ob Region; at the "Oktyabrskii" station it was 68.2–181 pairs/km^2 in 1978–1983 and 63.1–107.9 pairs/km^2 in 2002–2004. The average density for nine years of surveys was 105.3 ± 13.2 pairs/km^2. In the area of a spruce–birch forest, artic warblers nested with a local density of up to 3 pairs/ha in 1980 and up to 2 pairs/ha in other years. To the north, in a spruce–larch floodplain forest of the Khadytayakha River valley, the nesting density was no more than two pairs in the area of 14 ha, and the average density over the eight-year period was 8 ± 0.4 pairs/km^2 (Ryabitsev, 1993).

In the forest islands on the eastern slope of the Polar Urals, the maximum density values (58.5 ± 9.5 and 27.8 ± 10.2 (SE) pairs/km^2, SE is the standard error) were recorded in the upper reaches of the Longotyegan and Baidarata rivers, respectively (the northernmost forest island of larch woodlands) (Golovatyn and Paskhal'nyi 2005). In the woodlands of the Ob forest–tundra upland, the density of artic warblers was low; they did not nest regularly in the counting sites. At the "Kharp" station for 17 years of mapping, there were seven cases of recording one bird pair, always in sparse forests. In the tundra of Southern and Middle Yamal, artic warblers were found episodically in willow and alder forests.

Seasonal Phenomena of the Annual Cycle. Spring Migration

The artic warbler comes to the forest tundra among the last passerine birds in the first half of June. At the "Oktyabrskii" station, in the years of net catching (1978–1989), the first birds were caught between June 7, 1980, and June 15, 1983; the average date is September 9 ($n = 9$). At the beginning of the current century, despite the fact that the dates of ice drift at the Ob River, which involves the supply of heat with open water, shifted from the end of the third ten-day period of May to the end of the second ten-day period and the beginning of the third ten-day period, the arrival times for artic warblers almost did not change, but the arrival dates for willow warblers shifted to the middle of May (Ryzhanovskiy, 2014). The first artic warblers were encountered on June 7, 2002; June 2, 2003; and June 8, 2004 (Paskhal'nyi and Golovatin, 2007). However, in the exceptionally early spring of 1977 (the snow in the forest melted off at the end of April, a month earlier than usual), the first artic warbler began singing in the Sob River valley on May 19 and was caught on May 20. Only in 1982 did males and females appear in nets

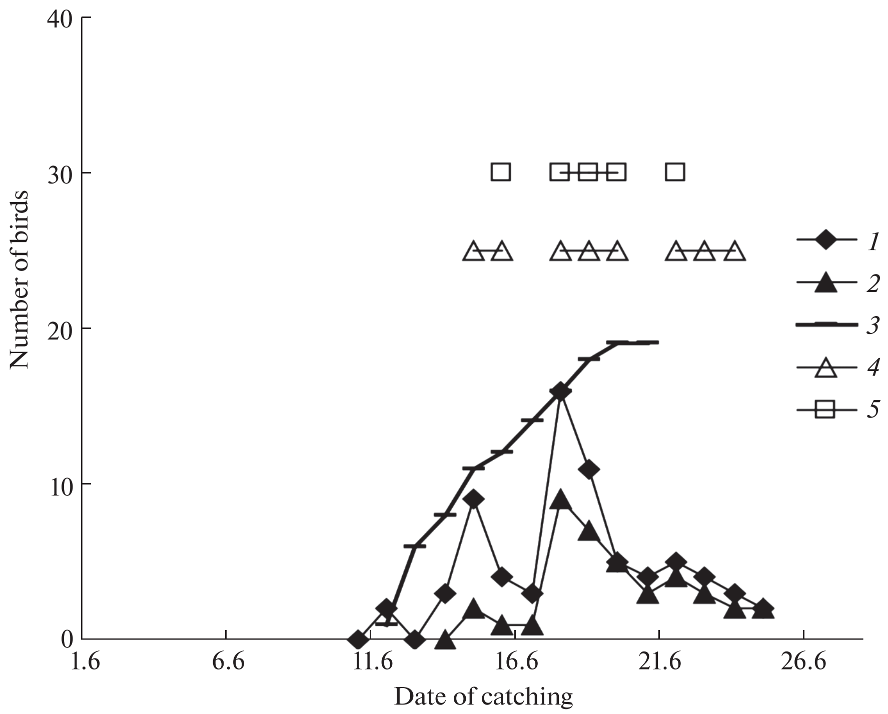

Fig. 1. Dynamics of the arrival of (*1*) males and (*2*) females, occupation of nesting sites by males (*3*) in June 1979, capture dates (one or more individuals) for (*4*) males and (*5*) females, which were ringed in previous years.

simultaneously, on June 10; in other years of the period 1977–1983, females began to be caught 3–6 days after catching the first male, on average 4.4 days after (n = 6). In 1979, among 179 artic warblers caught in June, there were 101 females (56.4%), and in other years the ratio was the opposite, 60–75% of males. The average daily air temperature on the day of catching the first male was 3.3–18.9°C, on average, 7.8°C, and on the day of catching the first female, it was 6–19°C, on average, 8°C (n = 7).

According to the results of net catching, the mass arrival lasted 7–15 days, on average, 10 days (n = 9). In 1978–1982, the number of artic warblers that were caught in spring with a constant line of six mist nets per 100 m line was 62–122, on average, 87.3 birds. A comparison of occupation of nesting sites at the "Oktyabrskii" station with the dynamics of arrival in 1979–1982 showed that the initial part of the migration flow included the artic warblers that had nested there in previous years (Ryzhanovskiy, 1984); moreover, up to 40% of males occupied the sites before active migration began.

The Formation of the Local Population

According to the results of the daily mapping of singing males that were subsequently encountered in the area, the local population formed over 11 days in 1979 (40 males, Fig. 1), over 18 days in 1980 (23 males), and over 4 days in 1980 (28 males). The first birds began singing in different parts of the control area, and the next birds filled empty areas.

Nesting Conservatism and Philopatry

Out of 106 chicks that were ringed in nests, two arctic warblers were found in the area the next year (1.88%). Out of 777 young arctic warblers that were ringed in the postnesting time, 14 arctic warblers were caught in subsequent years (1.8%). Given that the effectiveness of catching was 20% and mortality was 70% (Ryzhanovskiy, 1997), the area of birth became the place for repeated arrival for up to 30% of birds, the area of postnesting movements was chosen for repeated arrival by 80% of arctic warblers marked in the first ten-day period of catching (the end of July), 16.2% of arctic warblers marked in the second ten days (August), and 21% of arctic warblers marked in the third ten-day period of catching (August). Presumably, the connection with the territory of future nesting is formed at the age of 26–40 days.

Out of 24 male artic warblers that were caught near their own nests, seven birds were found in subsequent years at the site of the "Oktyabrskii" station (a return of 29.2%). Females were not observed to return to the site, but in spring the nets standing before the site caught fewer females than males: out of 294 ringed females, 21 (7.14%) were caught in subsequent years, and out of 368 ringed males, 35 (9.51%) were caught. Given the effectiveness of capture and mortality, the return of males and females was close to 100% and 80%, respectively.

Readiness for Reproduction

The weight (mg) of the testicles in the males that died in the nets was maximal as early as the first five days from the beginning of arrival, i.e., 136, 138, and 141; in the second five days, it was 105–176, on average, 123 ± 9.8 (n = 7); in the third five days, it was 115–150, on average, 128 ± 8.5 (n = 4). Thus, upon arriving in the forest tundra, artic warblers were ready for reproduction and did not need additional stimulation with the photoperiod of the Arctic Circle latitude.

Nesting

In the forest tundra, >80% of nests found were a niche that was dug in moss and covered with thin herbs, but always without feathers. This may be a mossy spot on the gentle slope of a bedrock bank, a moss hummock, a moss pillow on a ravine slope. Depending on the thickness of moss, a nest can be immersed in it completely or partially. The remaining nests were built into the holes and galleries of rodents or were on a level surface.

The first eggs in the season were laid at an air temperature of 5.6–21.8°C, on average 12.9°C (n = 5). Since in passerines the egg is formed for four days (Zimin, 1988), the air temperature in the preceding five-day period is important. For the arctic warbler, the average temperature during the period fluctuated within the limits of 5–12.9°C, averaged 10.5°C in different years, and was maximal in the group of passerines in the region (Ryzhanovskiy, 2001).

Artic warblers started to lay eggs on June 19, 1981; June 20, 1982; June 23, 1980; June 25, 1983; June 26, 1979; June 26, 1983; and June 28, 1978. Only in 1978 did the period of entry into reproduction last 17 days, up to July 15, and in the remaining years egg laying in the control nests began very synchronously, over 4–6 days. Repeated egg laying after devastation of nests was observed many times in the Subpolar Urals by Shutov (1988), and one case of clearly repeated egg laying was recorded in the Lower Ob Region.

Full clutches contained 3–8 eggs, on average, 6.01 ± 0.12 (n = 49), and most nests contained 6–7 eggs. In three nests found during the construction phase, females were incubating in the daytime after laying the fourth egg out of 6–7 eggs, i.e., continuous incubation started from the middle of egg laying. The incubation time from laying the first egg to hatching of the last chick was 18, 19, and 20 days, and the incubation time from laying the last egg to hatching of the first chick was 10, 12, and 13 days. Birds sat in the nest for 13–14 days, on average, 13.2 ± 0.19 days (n = 5). Nests were left by fledglings in the third ten-day period of July, and in one case a nest with a repeated clutch was left by fledglings on August 12. For eight nests, the duration of the period from laying the first egg to the nest being left by the last chick was 28–32 days, on average, 30 ± 0.5 days. In 1978, the period from laying the first egg in the season to the nest being left by the last fledgling in the season lasted 45 days (nine nests), in 1981 it lasted 37 days (18 nests), and in the years with the least number of nests, this period lasted 35–37 days.

Polygyny

In the Subpolar Urals, polygyny was observed in one field season (1980) out of five observation seasons (Shutov, 1986). At the "Oktyabrskii" station in 1981, two out of 17 males fed chicks in two nests. This is a simultaneous or harem polygyny, i.e., the first egg in both nests of the same male was laid on June 26, 1981.

Postnesting Migrations

According to the data of Shutov (1989), who studied the behavior of artic warbler fledglings at the "Oktyabrskii" station, they kept close to the nest in the first 4–5 days after departure, and at the age of 20–25 days, they were encountered at a distance of 150–200 m from the nest. At the age of 18–19 days, broods were divided into two groups with a constant composition, which broke up after reaching the age of 26–28 days. Out of the artic warblers ringed in nests, 52.5% of individuals (30 out of 58) left the control area. Two birds stayed in the nesting area for >32 days. The average length of stay in the environs of the nest after departure was 11.4 ± 0.7 days.

In the years of mass catches (1978–1981), a clearly pronounced peak of abundance was recorded 7–11 days after the first young birds appeared in nets; there were also several small peaks (Fig. 2). Out of 957 young artic warblers that were ringed in the Ob River valley, 57 birds (5.9%) were caught repeatedly. Almost all of them had been ringed in the first days of capture; i.e., they are local. The maximum duration of stay of such a bird in the area is 13 days, and the average one is 4.7 ± 0.4 days. In all years, the maximum number of birds (in nets) was recorded in the observation area in the first ten-day period of August. By the end of the ten-day period, the artic warblers marked in nests disappeared from the area, and the number of birds caught with nets sharply decreased. The artic warblers that were caught in the second ten-day period did not stay in the area (they were not caught repeatedly); i.e., they took part in migration, and the last individuals were caught by the beginning of the third ten-day period. Young birds that have left the nesting area have almost no time for a dispersion flight. It may be replaced by movement towards wintering places with short stops.

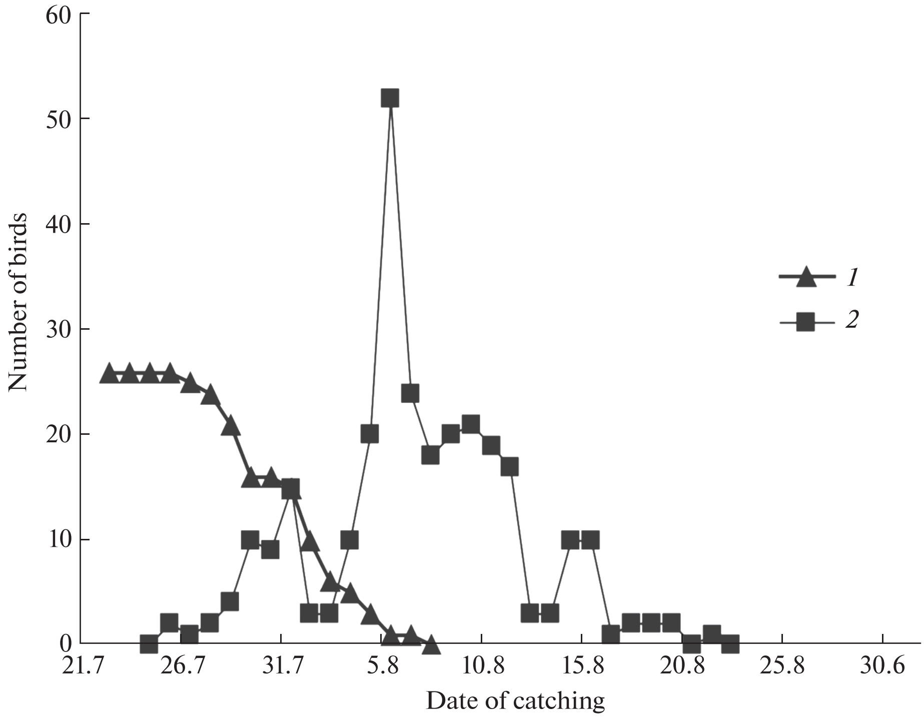

Fig. 2. Population dynamics in artic warblers in the postbreeding period in 1981. (*1*) Departure of the birds ringed in nests from the control area, (*2*) dynamics of catching artic warblers with nets and traps.

Molting

The young artic warblers that were caught in the Ob River valley did not start molting in 1978–1982) (plumage was described in 256 birds); postjuvenile molting was not observed in caged birds either. In the Sob River valley in 1976, plumage was described in late July–August in 120 birds, and none of them had started molting either. In 1977, until August 15, 189 warblers were caught without traces of molting, but from August 16 to 22, 15 out of 40 birds examined were recorded to have molting of the central rows of dorsal and ventral pterylae, and four birds had molting of thigh coverts (Ryzhanovskiy, 2015). In this case, we can distinguish the first stage of molting. This molting lasts no longer than ten days. In 2011–2014, none of 35 artic warblers caught and six caged ones had postjuvenile molting either. However, partial postjuvenile molting of the arctic warbler is known for Central and Eastern Siberia (Portenko, 1960; Bub, 1984).

Post-reeding molting is partial; it covers all contour plumage of the body, a part of the wing coverts, central tail feathers, and secondary flight feathers. In some birds, tail and flight feathers were not replaced. As a rule, postbreeding molting starts in the second ten-day period of July and partially coincides with nesting. Out of six artic warblers that were caught near nests, three males started molting before the departure of chicks; three females did not start changing plumage. In 1977, the first bird that started renewing plumage was caught on July 13. In other years, catching did not start before July 20, but by that time a significant part of the artic warblers examined had intensively replaced plumage. Birds without molting traces were caught on July 22, 1977; July 25 1978; and July 21, 1988. According to calculations, molting of arctic warblers annually started on July 10–15. Females started molting 7–10 days later than males. The period of entry into postbreeding molting in the birds of the Lower Ob population was extended to 15–25 days. The adult artic warblers that completed molting began to be caught at the end of the first ten-day period of August and in the second ten-day period of August. The last recording of an adult artic warbler in fresh plumage took place on August 24. Judging from repeated catches, molting of an individual lasts 20–25 days, and the molting season lasts no more than 40 days. Three arctic warblers that were caged until the next autumn started molting from June 10–July 5 and ended it on July 20–August 5. Molting was partial.

Complete replacement of plumage occurs in the winter. In the absence of postjuvenile molting in the nesting area, winter molting of first-year birds can be postjuvenile, transferred to the wintering part of the area, or prebreeding. The criterion for the determination is the response to change in the day length; a decreasing day length induces postjuvenile molting, and increasing day length leads to prebreeding molting (Noskov and Rymkevich, 1988). At our laboratory, molting of all three first-year birds started between February 25 and April 5, with an increase in the length of the day from 13S:11D at the end of January to 14S:10D at the beginning of March. Molting of a surviving individual lasted 45 days and ended on April 20 when day length was 15 hours. Thus, winter molting of first-year birds from Europe and Western Siberia is prebreeding, since it begins and proceeds with an increase in the length of the day.

Prebreeding molting in birds of the older age group (n = 5) began in the period from the second half of February to early March and lasted 63–70 days, on average, 64.6±0.19 days, and ended in the period from the third ten-day period of April to early May. On the wintering grounds, molting starts at the end of January and in February (Portenko, 1960). Molting is noted to be prolonged (Ptushenko, 1954), delaying the departure of a part of the birds from the wintering grounds until the middle of May.

Departure

Noskov and Rymkevich (1988), analyzing the transformation of annual bird cycles, came to the conclusion that postnesting movements could be transformed into migration in the case of postjuvenile molting being transferred to the wintering part of the area. Since molting of the West Siberian artic warbler is transferred to the winter period, a dispersion flight may be absent just for this reason, and after the breakup of broods birds quickly join migration. Therefore, the decrease in the number of first-year birds in nets can be considered as the beginning of migration. In the years of mass capture, it falls on August 10, 1977; August 16, 1978; August 12, 1979; August 10, 1980; and August 10, 1981. The period of departure lasted 11–14 days and ended in the third ten-day period of August, no later than August 26.

For 1977–1982, a positive correlation was found between the pairs of dates for the beginning of the hatching period/the beginning of departure ($r = 0.87 \pm 0.28$), the end of the hatching period/the beginning of departure ($r = 0.94 \pm 0.17$; the correlation was significant at $P \leq 0.05$). Departure started 29–35 days after hatching, on average, 43.2 days after it (Ryzhanovskiy, 1997). Adult birds with completed molting were caught from August 8 to August 24. All of them were not subsequently encountered; i.e., they began migration. The duration of stay of artic warblers in the nesting area of the subarctic part of Western Siberia (74–80 days, on average, 76.2 days (n = 4)) is minimal for passerines in our region (Ryzhanovskiy, 2005).

Out of three first-year birds that were kept in cages with daily activity recorders up to September 10, one bird first began to worry at night on August 20 at the age of 40 days; the second bird jumped on perches for four consecutive nights for 6–8 hours from August 28; the third one first began to worry on August 30 at the age of 50 days; and the fourth one jumped all night on September 8 (Ryzhanovskiy, 1997). Fat depositions that are indicative of the migratory status appeared in these birds at the age of 45–50 days, also in the third ten-day period of August. By this time, local first-year birds had left our region, i.e., the southern migration flow had been formed earlier than the night activity and fat deposition began.

The period of migratory obesity in the first-year birds that had been caged in winter lasted 90, 96, and 105 days, until mid-November and early December. In the caged adult artic warblers, obesity started simultaneously with the end of postbreeding molting, in the second ten-day perido of August, and lasted 60–105 days, on average, 85.6 ± 5.6 days (n = 8), until the second half of October to late November. Artic warblers may arrive in the wintering grounds in late October and November.

RESULTS AND DISCUSSION

Arctic warblers are as common in the floodplain forests of the Ob forest tundra as willow warblers are. In the southern subarctic tundra of the Yamal, arctic warblers are rare, while willow warblers are not abundant either, and in the northern subarctic tundra, willow warblers have become rare. The northern boundary of the willow warbler range in the Yamal is at a distance of no more than 150 km from the boundary of the artic warbler range. In Central Siberia, the limits of forest tundra and shrub tundra have shifted to the north by almost 200 km, and the limits of the spread of warblers have also shifted to the north. In the Taimyr, the willow warbler nests along the shores of Yenisei Bay (71° N) (Rogacheva, 1988), and the artic warbler is common in larch woodlands near the settlement of Khatanga (72° N) (Volkov, 1987). In Eastern Taimyr, willow warblers were common, and artic warblers were not abundant at the Ary-Mas tract (71°30′ N) (Chupin, 1987). Thus, the northern limits to which the artic warbler has penetrated into Western and Central Siberia are determined by the presence of woody and tall shrub vegetation, whereas the spread of the willow warbler is limited by the boundary of the low shrub area (Ryzhanovskiy, 2014).

The study of the trophic relationships of warblers in Southern Yamal (Golovatin and Kolbin, 1986) revealed a great similarity of the willow warbler and arctic warbler in the taxonomic composition of invertebrates and the size of food objects. Most likely, the height (>2 m) and density of shrubs or biomass of arthropods are important to artic warblers in choosing the nesting area in the tundra zone, since, having the same area, tall shrub grounds are more abundant in food than low shrub grounds, or both factors are important, but not the species composition of food objects.

Many birds of the tundra zone of Western Siberia were shown to have similarity of the southern and northern boundaries of ranges with the isotherms of summer months. The artic warbler was found to have similarity of the northern boundary with the isotherm of the surface air layer that was ~3°C in June and ~8°C in July (our calculations); for the willow warbler, the boundary of the range is close to the isotherm that is ~0°C in June (our calculations) and ~6°C in July (Zhukov, 2013). In the Ob Region and in Southern Yamal, the average long-term temperature on the day of catching was ~7.8°C for the first male artic warbler, ~8°C for the first female artic warbler, ~2.3°C for the first male willow warbler, and ~2.2°C for the first female willow warbler.

The timing and duration of seasonal arrivals of birds in the middle and high latitudes partially depend on the distance from wintering grounds (Zimin, 1988). Willow warblers started to arrive in the northern part of Western Siberia in 1978–1982 8–20 days earlier than the first artic warblers did (on average, 12 days earlier). In Eastern Europe, the gap between the timing of arrival is even greater: willow warblers arrive in the Leningrad oblast in late April and early May, the average date of the appearance of males is May 3 (Mal'chevskii and Pukinskii, 1983), and the first artic warblers arrive in Finland in the middle of June (Atlas, 2003). In the Far East, these warblers appear in spring in the first half of May, after the foliage comes out (Panov, 1973); near the city of Krasnoyarsk, the earliest meeting took place on May 31 (Yudin, 1952), also in the phenological summer. It is only in the north of the range where artic warblers arrive in late spring, before the foliage comes out, but at higher air temperatures in comparison with those during the arrival of willow warblers. The Putorana Plateau is approximately at an equal distance from Tropical Africa and Southeast Asia. For Kapchug Lake, the first willow warblers arrive there a week earlier than artic warblers: on May 28 and May 4, 1988; on June 9 and June 16, 1989, respectively (Romanov, 1996). Undoubtedly, artic warblers are more exacting with respect to temperature and (or) phenological conditions at the time of arrival, while the level of requirements to external conditions decreases with advancement to the Subarctic Region, which may be due to the greater readiness of the gonads for reproduction, since they arrive with fully developed testicles. Male willow warblers arrive in the forest tundra with the testicles that have not reached the maximum size, so they need additional photostimulation with the polar day, which has been proven experimentally (Ryzhanovskiy, 2001).

Arriving in the forest tundra on average 12 days later than willow warblers, artic warblers began laying eggs on average 6.8 days ($n = 6$) later. The egg-laying season is shorter in artic warblers than in willow warblers, since artic warblers rarely nest repeatedly. This may be due to the polar day in July; artic warblers have adapted to the photoperiod of middle latitudes with alternation of light and dark phases, and they only start to adapt to high latitudes; therefore, the twenty-four-hour day length induces not only faster growth of the gonads, but also faster onset of "gonad fatigue" (Danilov, 1966). Willow warblers have settled in the Subarctic Region and adapted to the polar day. Probably, repeated nesting is more common for this reason.

In the Lower Ob Region, clutches of the willow warbler and artic warbler are equal (6.1 eggs in each), and the incubation and feeding times are also equal (29.6 and 30 days, respectively), but, due to repeated egg laying, the breeding season in the willow warbler lasts longer than in the artic warbler (44–59 and 35–45 days, respectively, in different years). The average lengths of stay of young willow warblers and artic warblers in the environs of the nest were almost equal in the forest tundra (10.9 ± 0.8 and 11.4 ± 0.9 days, respectively), but closer to the wintering grounds in the Kurshskaya Spit (Sokolov et al., 1986), willow warblers stayed in the environs of their nests significantly longer, for 24±1.5 days after leaving the nests. The artic warblers of the Ob Region do not have a dispersion flight; they start migration at the age of 25–35 days. First-year birds fly away from Finland in early August (Atlas, 2003), possibly forming brood groups. Willow warblers were noted to have a dispersion flight and subsequent stop for postjuvenile molting. In Eastern Europe, dispersion flight starts ten days later than in Siberia, and a subsequent stop for molting must last longer since molting is more complete. Molting is even more complete in first-year willow warblers in Western Europe (Norman, 1981), closer to the wintering area. Artic warblers were noted to have postjuvenile molting in Central Siberia (Bub, 1984) and Yakutia (Portenko, 1960), also closer to the wintering area, but the Far Eastern artic warblers do not have it (Medvedeva, 2011).

Postbreeding molting in the artic warbler is partial; it is likely that the central tail feathers and tertiary flight feathers are very rarely replaced throughout the area. Most willow warblers in the Lower Ob Region and Eastern Europe have complete postbreeding molting. In the Ob Region, 31.2% of willow warblers did not replace a part of the internal secondary flight feathers; in the Ladoga Region, they were not replaced by 8.3% of them (Lapshin, 1990); i.e., the proportion of willow warblers with incomplete molting decreases with the approach of wintering areas.

Willow warblers leave our region to go to the wintering area in Tropical Africa; they fly through the Middle East (a willow warbler with our ring was found in Israel), i.e., almost in a straight line to the south-southwest. Artic warblers fly sublatitudinally over the taiga to a distance of >3000 km, and only in Eastern Siberia do they turn to the south, in the direction of wintering areas. Migration over the taiga lengthens the path and complicates the conditions of flight, since autumn begins in Siberia in late August. Therefore, Fennoscandia is left by artic warblers in early August, and the Ob Region is left by them in the middle of August. For Scandinavian artic warblers, it is assumed that it is just a very long migration path that is maximal for the passerines of Fennoscandia, which reduces the possibilities for the further spread of the species to the northwest (Atlas, 2003). The same can be assumed for the willow warblers nesting in Yakutia, which have the longest (>10000 km) migration path, but have not reached the eastern limits of the taiga.

Migratory obesity in the caged artic warblers lasted longer than in willow warblers: 60–105 days, on average, 85.6 ± 5.6 days ($n = 8$) and 60–80 days, on average, 72.1 ± 2.5 days ($n = 8$), which corresponds to a larger migration distance. The wintering areas must be reached by both species predominantly in November. Winter molting in both species is prebreeding and complete according to the position in the annual cycle; it proceeds with an increase in the day length from the middle of January and late January to early April and the middle of April; the individual molting time is ~2.5 months. During wintering at the subequatorial latitudes, the entry into molting is induced in both species by the minimum increase in day length; molting proceeds with a subsequent slow increase, and, therefore, its rate is low.

The advancement of the willow warbler into the tundra zone, which has been recorded in recent decades (Ryzhanovskiy, 2014), is almost not observed in the artic warbler. The species has stopped at the border of the tall shrub area.

CONCLUSIONS

The artic warbler and willow warbler are settling in Northern Eurasia at various paces, moving towards each other and partially competing for food. Arctic warblers are thermophilic; therefore, they arrive in the Subarctic Region later than most passerines, at the end of spring. The nesting season is short due to repeated egg laying being rare. The early departure of artic warblers to wintering areas is ensured by the absence of postjuvenile molting, reduction in the completeness and duration of postbreeding molting, and refusal of postbreeding migrations. All this reduces the season of stay of artic warblers in the northern part of Western Siberia to the minimum among migratory passerines. The long spring and autumn migrations over the taiga are assumed to be the main reason for the reduction of the season.

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REFERENCES

Atlas gnezdyashchikhsya ptits Evropy evropeiskogo soveta po uchetam ptits (Atlas of Breeding Birds in Europe of the European Council on Counting Birds), Rogacheva, E.V. and Syroechkovskii, E.E., Eds., Moscow: IPEE RAN, 2003.

Bub, H., *Kennzeichen und Mauser europaischer Singvogel*, Wittenberg: Lutherstadt, 1984, vol. 3.

Chupin, I.I., Birds of the forest island Ary-Mas (Eastern Taimyr), in *Fauna i ekologiya ptits i mlekopitayushchikh Srednei Sibiri* (Fauna and Ecology of Birds and Mammals in Central Siberia), Moscow: Nauka, 1987, pp. 39–53.

Danilov, N.N., *Puti prisposoblenii nazemnykh pozvonochnykh zhivotnykh k usloviyam sushchestvovaniya v Subarktike* (Ways of Adaptation of Terrestrial Vertebrates to the Subarctic Conditions), vol. 2: *Ptitsy* (Birds), *Tr. Inst. Biol.*, Sverdlovsk: Ural. Rabochii, 1966, no. 56.

Danilov, N.N., Ryzhanovskiy, V.N., and Ryabitsev, V.K., *Ptitsy Yamala (Birds of Yamal)*, Moscow: Nauka, 1984.

Deryugin, K.M., Traveling into the valley of the middle and lower reaches of the Ob River and the fauna of this area, *Tr. St. Petersb. Obshch. Estestvoispytat. Otd. Zool. Fiziol.*, 1898, vol. 29, no. 2, pp. 47–140.

Formozov, A.N., The plain pattern of Western Siberia and the features of the fauna associated with it, in *Razvitie i preobrazovanie geograficheskoi sredy* (Development and Transformation of the Geographical Environment), Moscow: Nauka, 1964, pp. 201–221.

Golovatin, M.G. and Kolbin, V.A., Influence of trophic relationships on the abundance of some passerine birds in the northern taiga of the Polar Urals, in *Regulyatsiya chislennosti i plotnosti populyatsii zhivotnykh Subarktiki* (Regulation of Population Abundance and Density of Subarctic Animals), Sverdlovsk: UNTs AN SSSR, 1986, pp. 119–129.

Golovatin, M.G. and Paskhal'nyi, S.P., *Ptitsy Polyarnogo Urala* (Birds of Polar Urals), Yekaterinburg: Izd. Ural. Univ., 2005.

Kucheruk, V.V., Kovalevskii, Yu.V., and Surbonos, A.G., Changes in the population of birds of the fauna of Southern Yamal in the last 100 years, *Byul. Mosk. Obshch. Ispytat. Prirody. Otd. Biol.*, 1975, vol. 80, no. 1, pp. 141–148.

Lapshin, N.V., Willow warbler *Phylloscopus trochilus* (L.), in *Lin'ka vorob'inykh ptits Severo-Zapada SSSR* (Molt of Passerine Birds of the North-West of the USSR), Leningrad: Izd. LGU, 1990, pp. 114–120.

Mal'chevskii, A.S. and Pukinskii, Yu.B., *Ptitsy Leningradskoi oblasti i sopredel'nykh territorii* (Birds of Leningrad Oblast and Adjacent Areas), Leningrad: Izd. LGU, 1983, vol. 2.

Medvedeva, E.A., Molt and its place in the annual cycle of some species of passerine birds of the south of the Far East, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Vladivostok: Biol.-Pochv. Inst., 2011.

Norman, S.C., A study of post-juvenile moult in willow warblers, *Ringing Migr.*, 1981, no. 37, pp. 165–172.

Noskov, G.A. and Rymkevich, T.A., Methods of study of intraspecific variability of molt in birds, in *Metodika issledovaniya produktivnosti i struktury vidov v predelakh ikh arealov* (Method of Study of Productivity and Structure of Species Within Their Ranges), Vilnius: Moklas, 1977, vol. 1, pp. 37–48.

Noskov, G.A. and Rymkevich, T.V., Patterns of adaptive changes in the annual cycle of birds, *Dokl. Akad. Nauk SSSR*, 1988, vol. 301, no. 2, pp. 505–508.

Panov, E.N., *Ptitsy Yuzhnogo Primor'ya* (Birds of Southern Primorye), Novosibirsk: Nauka, 1973.

Paskhal'nyi, S.P. and Golovatin, M.G., Spring migration of birds in the lower reaches of the Ob River, in *Ekosistemy Subarktiki: struktura, dinamika, problemy okhrany* (Subarctic Ecosystems: Structure, Dynamics, and Conservation Problems), *Nauch. Vestn. YaNAO*, 2007, no. 6 (50), part 2, pp. 23–57.

Portenko, L.A., *Ptitsy SSSR* (Birds of the USSR), Moscow: Izd. AN SSSR, 1960, part IV.

Ptushenko, E.S., Genus Phylloscopus, in *Ptitsy Sovetskogo Soyuza* (Birds of the Soviet Union), Moscow: Sov. Nauka, 1954, vol. 6, pp. 145–207.

Ravkin, E.S. and Ravkin, Yu.S., *Ptitsy ravnin Severnoi Evrazii: chislennost', raspredelenie i prostranstvennaya organizatsiya soobshchestv* (Birds of Plains of Northern Eurasia: Abundance, Distribution, and Spatial Organization of Communities), Novosibirsk: Nauka, 2005.

Rogacheva, E.V., *Ptitsy Srednei Sibiri. Rasprostranenie, chislennost', zoogeografiya* (Birds of Central Siberia: Distribution, Abundance, and Zoogeography), Moscow: Nauka, 1988.

Romanov, A.A., *Ptitsy plato Putorana* (Birds of the Putorana Plateau), Moscow: Rossel'khozakademiya, 1996.

Ryabitsev, V.K., *Territorial'nye otnosheniya i dinamika soobshchestv ptits v Subarktike* (Territorial Relations and Dynamics of Bird Communities in the Subarctic), Yekaterinburg: Nauka, 1993.

Ryzhanovskiy, V.N., Spring migration of willow and arctic warblers at the northern boundary of the range, *Dokl. Vyssh. Shk. Biol. Nauki*, 1984, no. 9, pp. 46–51.

Ryzhanovskiy, V.N., *Ekologiya poslegnezdovogo perioda zhizni vorob'inykh ptits Subarktiki* (Ecology of Post-Nesting Period of Life of Subarctic Passerine Birds), Yekaterinburg: Izd. Ural. Univ., 1997.

Ryzhanovskiy, V.N., Breeding season as part of the annual cycle of subarctic passerine birds, in *Gnezdovaya zhizn' ptits* (Nesting Life of Birds), Perm: Permsk. Gos. Ped. Inst., 2001, pp. 3–22.

Ryzhanovskiy, V.N., Timing and duration of the seasonal phenomena of the annual cycle of life of subarctic passerines as exemplified by the birds of the Lower Ob region, *Sib. Ekol. Zh.*, 2005, no. 3, pp. 475–487.

Ryzhanovsky, V.N., Adaptive features of the ecology and annual cycle of the willow warbler (*Phylloscopus trochilus* L.) at the northern boundary of the Siberian part of the range, *Biol. Bull.* (Moscow), 2014, vol. 41, no. 6, pp. 529–539.

Ryzhanovskii, V.N., Annual molt cycle of arctic warbler (*Phylloscopus borealis*) from northwestern Siberia and its geographic variation, *Russ. J. Ecol.*, 2015, vol. 46, no. 6, pp. 579–584.

Shukhov, I.N., Birds of Obdorsk krai, *Ezhegodnik Zool. Muz. Imper. Akad. Nauk*, St. Peterburg, 2015, vol. 20, no. 2, pp. 167–238.

Shutov, S.V., Polygyny of willow warbler and Arctic warbler in the Polar Urals and its role in maintaining abundance, in *Regulyatsiya chislennosti i plotnosti populyatsii zhivotnykh Subarktiki* (Regulation of Population Abundance and Density of Subarctic Animals), Sverdlovsk: UNTs AN SSSR, 1986, pp. 71–77.

Shutov, S.V., Population ecology of willow warbler and Arctic warbler in Southern Subarctic, *Cand. Sci. (Biol.) Dissertation*, Sverdlovsk: IERiZh UrO RAN, 1988.

Shutov, S.V., Territorial conservatism, dispersion of common species of passerines in the cis-Polar Urals, and some patterns of their latitudinal changes, *Ekologiya*, 1989, no. 4, pp. 69–74.

Shutov, S.V., Breeding density of common species of passerine birds (Passeriformes) in the Polar Urals and some patterns of its spatial variation in the floodplains of South Subarctic, *Zool. Zh.*, 1990, vol. 69, no. 5, pp. 93–99.

Sokolov, L.V., Lapshin, N.V., and Rezvyi, S.P., Territorial behavior of willow warbler on the Curonian Spit of the Baltic Sea and in the southeastern Ladoga region, in *Aktual'nye problemy ornitologii* (Actual Problems of Ornithology), Moscow: Nauka, 1986, pp. 190–206.

Vartapetov, L.G., *Ptitsy severnoi taigi Zapadno-Sibirskoi ravniny* (Birds of Northern Taiga of the West Siberian Plain), Novosibirsk: Nauka, 1998.

Volkov, A.E., Materials on the fauna and population of birds of the upper reaches of the Khatanga River and the environs of the Khatanga Village, in *Fauna i ekologiya ptits i mlekopitayushchikh Srednei Sibiri* (Fauna and Ecology of Birds and Mammals of Central Siberia), Moscow: Nauka, 1987, pp. 91–107.

Yudin, K.A., Observations on the distribution and biology of birds of the Krasnoyarsk krai, in *Tr. ZIN SSSR* (Transactions of the Zoological Institute of the USSR), Moscow: Izd. AN SSSR, 1952, vol. 9, no. 4, pp. 1028–1060.

Yudkin, V.A., *Ekologicheskie aspekty geografii ptits Severnoi Evrazii* (Ecological Aspects of the Geography of Birds of Northern Eurasia), Novosibirsk: Nauka, 2009.

Zhukov, V.S., Similarity of boundaries of ranges of birds with isotherms of summer months in the tundra zone of the West Siberian Plain, *Povolzh. Ekol. Zh.*, 2013, no. 1, pp. 16–28.

Zimin, V.B., *Ekologiya vorob'inykh ptits severo-zapada SSSR* (Ecology of Passerine Birds of the North-West of the USSR), Leningrad: Nauka, 1988.

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SPELL: 1. mealworm