ISSN 1062-3590, Biology Bulletin, 2023, Vol. 50, No. 6, pp. 1401–1410. © Pleiades Publishing, Inc., 2023.
Russian Text © The Author(s), 2023, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2023, No. 6, pp. 706–715.

ECOLOGY

Ecology of the Brambling *Fringilla montifringilla* L. in the Northern Part of Western Siberia

V. N. Ryzhanovsky*, **

Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia
**e-mail: ryzhanovskiy@ya.ru*
***e-mail: ryzhanovsky@ipae.uran.ru*

Received March 17, 2022; revised May 18, 2023; accepted May 19, 2023

Abstract—The features of the ecology of bramblings at the northern limit of their range in the Priobskaya forest tundra are considered. The nesting density remains high, locally 50–100 pairs/km^2, up to the boundary of the distribution of coastal forests and floodplain woodlands along the 67th parallel. Habitats suitable for nesting bramblings are also available to the north, but birds are few in number. The biotopic conditions do not significantly limit the progress to the north. The bramblings have no adaptations to Subarctic conditions. This is a medium- and north-taiga species that develops the forest tundra as it warms and thickens the woodlands.

Keywords: Forest tundra, brambling, habitat, ecology, reproduction, molting

DOI: 10.1134/S1062359023602847

INTRODUCTION

The brambling is a common nesting migratory bird in the forest and forest–tundra landscapes of Northern Eurasia; therefore, many avifaunal reports on the regions of Russia contain essays on the ecology of this species. A common property of these essays is the fragmentation of the material on the basis of which they are written. As a rule, there is no discussion of the adaptive features of ecology that allow brambling populations to exist in one part of the range or another. The materials at my disposal were collected on the northern border of the species range, in the Priobskaya forest–tundra. A combination of different collection methods like trapping with nets and traps with live processing and marking and retrapping, maintenance of bramblings in captivity under different photoperiodic conditions, counts on test plots, observations, and a long period of research have made it possible to consider the features of the life of bramblings at the northern limit of the range in more detail than was done earlier, including in our (Danilov et al., 1984) summary. Since the range of bramblings includes the Subarctic, adaptations to the development of the Arctic are of undoubted interest, which is also a task of this work.

MATERIALS AND METHODS

The main study area is the Ob River valley in the vicinity of the city of Labytnangi (Oktyabrskii station, 66°40′ N 66°40′ E) and the middle course of the Sob River in the Polar Urals (Krasnyi Kamen’ railway station, 66°40′ N 66°30′ E), where in 1976–1989, 2002–2004, and 2016–2018 we searched for and surveyed nests and caught young and adult bramblings, including birds previously ringed during the nesting period. In the same place, chicks were recruited for feeding and further maintenance under different photoperiodic conditions. There is a limited amount of data on nesting (68 nest cards), data on trapping birds with cobwebs and a large cone trap, the results of daily bird counts on a plot of 24 ha in 1978–1983 during the occupation of territories, and on the territory of 36 hectares in 2002–2004; the results of route counts of birds in the Sobi Valley in 1977 and 2002–2004 and the results of autopsy of birds that died in nets; and materials of experiments on keeping adults and young bramblings in captivity under different photoperiodic conditions. When determining the dates of the start of oviposition, we used information on the nests found during the laying of eggs and on the timing of the hatching of the first chick. The duration of incubation was determined by the nests found with incomplete clutches, and the duration of feeding was determined by the dates of hatching of the first chick and the departure of the last fledgling from the nest.

The description of the state of plumage was carried out according to the method of Noskov and Rymkevich (1977), where a complete scheme of the arrangement of pterylae and their divisions is given. Analysis of a very extended process of plumage replacement requires its division into a number of steps or stages (Blumenthal and Dolnik, 1966). In bramblings, with a complete post-nuptial molt, 11 stages are distinguished, and with a partial post-juvenile molt, seven

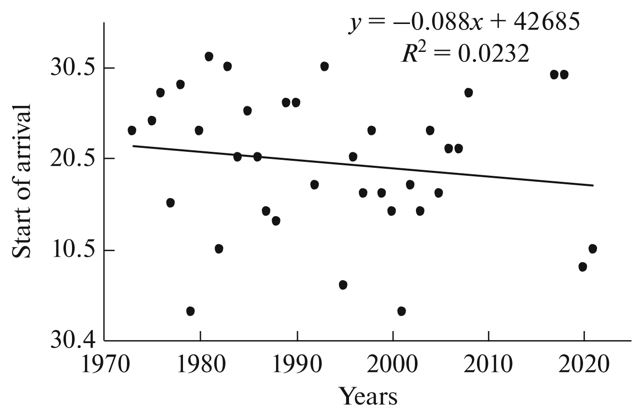

Fig. 1. Arrival dates, trend line, and equations.

stages. The average seasonal dates of the beginning, end, and duration of molting in nature were determined using regression equations (Pimm, 1976) of the Microsoft® Excel 2002 program.

Part of the bramblings kept in the summer period (five one-year-olds and six males over a year old) were transported to the laboratory in autumn, where the birds were kept until the next summer. All of them had their weight and fat content determined every ten days; four first years were kept in cages with jump counters and two, in cages with night disturbance recorders. The laboratory room had small windows, so electric lamps burned in the laboratory for ten hours. When in October the length of the day outside the window was reduced to 10L : 14D and continued to decrease further, the photomode in the cells remained unchanged until mid-March, i.e., until the length of the day exceeded ten hours of light.

RESULTS AND DISCUSSION

Spatial and biotopic distribution. In Western Siberia, the brambling breeds from the southern border of the taiga zone to the northern tip of the insular and floodplain forests of the forest–tundra zone at 67°–68.5° N on the Yamal Peninsula, the northernmost nesting points of which are the upper reaches of the Yadayakhodayakha and Khadytayakha rivers and left tributaries of the Shchuchya (Danilov et al., 1984) and Baydarata rivers (68° N). Along the slope of the Polar Urals, the species penetrates to the headwaters of the Baidarata River (68° N). Here the bramblings inhabit tall willows and alder curtains. At the same time, they prefer thickets where individual trees grow, and forest areas on mountain slopes were preferable to coastal forests (Golovatin and Paskhalny, 2005). To the south, bramblings are common inhabitants of the forests of river valleys, where they choose mixed sparse stands of alder, birch, and spruce. Larch forests are less successful; bramblings apparently avoid larch woodlands, because in the larch forests of the Kharp forest–tundra station (near the town of Labytnangi), no more than one pair occasionally nested for many years (Danilov et al., 1984).

The nesting density depends on the biotope, and in some places it can be high. A significant amount of information on the density of bramblings in different types of habitats in the Polar Urals is given by Golovatin and Paskhalnyi (2005): from 1.4 ± 0.4 pairs/km² in thickets of tall shrubs to 35.4 ± 4.2 pairs/km² in park-type forests, 41.6 ± 5.5 pairs/km² in forests of mountain slopes, locally, 52 ± 14.4. In the Sob River valley in 1977, bramblings nested at a density of 51 pairs/km² in the area of mixed forest (137 km); in 2002 and 2003 at the Krasnyi Kamen Railroad station (141 km), it was 16.3–33.3 pairs/km² (Ryzhanovsky and Paskhalyi, 2007).

In South Yamal, in the floodplain forest of the Khadytayakha River, in various years (n = 8), bramblings nested at a density of 28.6–35.7, averaging 33.0 ± 1.3 pairs/km² (Ryabitsev, 1993). In the valley of the middle reaches of the Shchuch'ya River in 1973, the nesting density was 10 and 20 pairs/km² (Kucheruk et al., 1975). At the Oktyabrskii Station in 1978–1983 from 36.4 to 81.8 pairs/km² were recorded, and in 2002–2004, 42.1–73.6 pairs/km², with an average density over an 8-year period of 62.8 ± 5.7 pairs/km². On the border of the forest–tundra and the northern taiga, on the territory of the Voikar station, the average density over 15 years of observations was 22.6 ± 3.0 pairs/km². In the northern and middle taiga of the Ob–Yenisei interfluve, the nesting density of brambling is usually not higher than in the forest–tundra: 46–56 individuals/km² (Vartapetov, 1998) and is lower than in the northern taiga of the western slope of the Subpolar Urals, 60 ± 5.8 pairs/km² (Shutov, 1990).

Spring migration. At the latitude of the Arctic Circle, arrival always began in May, between May 3 and May 29. The average date of arrival of the first bramblings for 38 years is May 19. The arrival begins with a daylight duration of at least 17 hours 40 minutes (beginning of May), but more often at 20 or more hours of light. According to Paskhalnyi (2002), the brambling belongs to the species that in the years 1986–2002 began to appear earlier than in the previous 15 years (1970–1985). The shift in the average date of arrival in the area of Labytnangi was five days: May 21 and May 16, respectively. However, in the past five years of observations (2016–2021), the arrival to the territory of the garden of the Arctic Station, Ural Branch, Russian Academy of Sciences, began between May 8 and May 29, on average, May 18 (Shtro, personal communication). Thus, there is no stable shift in the start of arrival to earlier dates due to global warming; the shift trend, taking into account the latest dates, is not reliable (Fig. 1).

The appearance of the first bramblings was observed 1–3 days before the main May warming,

Table 1. Sex ratio in nets and traps during arrival in different years

Sex	Year									
	1978	1979	1980	1981	1982	1983	1986	1987	1988	1989
Male	90	125	30	35	83	24	127	38	36	38
Female	65	55	15	17	67	21	81	24	20	21

during which the majority of passerine species from the forest–tundra begin to arrive. The average daily air temperature on the day of encountering the first bird in the season ranged from –3.2° up to 10.3° C, on average, 2.4°C (n = 34). During the analyzed time series (1971–2020) there is an unreliable increase in air temperature on the first day of arrival of the bramblings.

According to the results of trappings with nets (1977–1983) and traps (1987–1989), the period of passage of bramblings to the north lasted 11–36 days, averaging 21.6 days. Since the birds migrated through the forest strip, in the lower part of which in 1978–1982 a line of nets 50–70 m long stood at a constant position; the total number of bramblings that should have been caught by a 100-meter line during the arrival period was calculated. Their maximum number, 275 bramblings, should have been caught in 1978, in the subsequent years 1979–1982, 73, 50, 65, and 67 birds, respectively, should have fallen into the nets. It should be noted that the spring of 1978 was notable for the late, friendly, and massive arrival of many forest and shrubby passerines: in terms of 100 m of nets, 4107 passerines were caught in that spring compared to 512–715 birds in subsequent years. Bramblings in 1978 may have been carried north by a wave of mass migration of the common red-poll, which accounted for 69% of the flow. In subsequent years, common redpolls were few in number, and the number of flying bramblings decreased and remained at the same level.

There are no significant differences in terms of arrival of males and females. During the ten-year period of trapping at the Oktyabrskaya station, males appeared 1–3 days earlier than females for four years; in 1981, a female was caught first; in other years, the first males and females were caught simultaneously. Only in 1983, in the first and second ten-day periods from the beginning of arrival was the sex ratio almost equal; in other years, males dominated (Table 1). In total, for all the years in the first two ten-day periods of arrival, 615 males and 384 females were caught. The proportion of males by five days was 61.2, 63.5, 61.2, and 56.6%, and the proportion of males by years was 54.5–71.4, on average, 64.2% (n = 10).

In male bramblings, by contrast in the coloration of the large upper coverts of secondaries in spring and summer, one can separate the first years from birds older than a year. Out of 304 males examined for all years of the arrival period with a registered age, there were 179 first-years (58.9%). Paevsky (2008) indicates a slight predominance of one-year-olds during the spring migration of bramblings through the Curonian Spit. He also provides information about the dominance of bramblings of older age groups during the first five days of migration. In the Lower Ob region, in the first ten days from the date of arrival, out of 113 birds, there were 57 males older than one year of age (51.4%); in the second decade, out of 70 birds, 28 (40%) were older than a year, which coincides with the data of Paevsky (2008).

Among the bramblings caught in the spring, females with brood spots were periodically encountered, and they were recorded already in the first days of arrival, in late May and early June, when only males occupied nesting sites (Ryzhanovsky, 2008). These were birds in the second (oviposition phase) and fourth (chick-feeding phase) stages. The proportion of such birds could be significant. In particular, in 1988, out of 18 female bramblings, eight birds had brood spots; in 1989, six out of 15 did; in 1981, four out of 12; in 1983, two out of 28, and in 1986, two out of 83. In 1978, 1980, 1982, and 1987, we did not catch such birds. As a rule, birds with brood spots were caught in nets and traps as part of a flock, in which the sex ratio was almost equal. For example, on June 10, 1981, a flock of eight bramblings was caught with a net: four males and four females with spots of stage 4. In 1989, on the third day from the beginning of the arrival, a flock of bramblings was caught, including 14 males and ten females, of which six females also had brood spots of the 4th stage.

The coincidence of the seasons of the presence and absence of brood spots in the common red-poll (*Acanthis flammea*) and bramblings was noted, which is more realistic under climatic impacts covering large areas (Ryzhanovsky and Ryabitsev, 2021). It can also be assumed that birds at the first or second stages attempted to nest in the northern taiga and southern forest–tundra, and those at the 4th stage, in the middle taiga. It is possible that pairs of bramblings do not break up after an unsuccessful nesting attempt, but migrate further north.

The first wave of arriving birds, judging by their fatness, includes individuals with a developed migratory state. In the first ten days of arrival, the fatness of 21 birds (8.7%) was assessed as "high"; 33.4% had medium fat; and the rest were categorized as lean and low fat. In the second ten-day period, the proportion of well-fed bramblings decreased to 2.7%; the proportion of medium-fat birds did not change (35.2%), and in the subsequent days of the summer we did not catch very fat birds anymore; the proportion of medium-fat birds in different ten-day periods of summer fluctuated between 0 and 10% (Ryzhanovsky, 2004).

Occupation of territories and formation of pairs. Males occupied areas starting from the first wave of arrival. In 1980, the local population of the site was formed in 21 days; in 1981, in ten days; and in 1982, in 20 days. In all cases, the males that occupied the sites and marked them repeatedly are considered. It is assumed that these are the same birds. In some years, as the experiments of Ryabitsev (1993) showed, bramblings flew to the northern limit of the range, to the Khadytayakha floodplain, in abundance: after shooting a pair, the vacated territory was reoccupied, sometimes after several minutes, but in other years the liberated territories were not occupied. The territory can be occupied by pairs of birds formed on migration (Ryabitsev, 1993) or during the first nesting attempt, as suggested above.

The brambling belongs to species with weak territorial attachment. Ryabitsev (1993) received no returns from 17 birds nesting in the Khadytayakha valley. Five out of 97 adult bramblings returned to the Subpolar Urals (Shutov, 1989). In Swedish Lapland, one adult returned out of 262; none of the 434 chicks returned (Lindström, 1987). None of the 149 adults and 34 juveniles returned to the Sobi valley; in the following years, after tagging, none of the 1175 adults, 52 juveniles, or 35 tagged in the nests were caught at the Oktyabrskaya station.

Nesting. Bramblings arrive with fairly developed gonads; males have a well-developed cloacal protrusion. On the first five days from the beginning of arrival, for the males shot or killed in the nets ($n = 7$), the gonads had a weight of 315–429 mg, 382 ± 16.5 mg on average; in the second five-day period, 270–460, on average, 351 ± 26.0 ($n = 8$); and on the fourth five-day period, the testis of one male weighed 470 mg. Cloacal protrusions of maximum size were observed in birds caught from flocks on the fourth five-day period (ten out of 23), i.e., males arriving at the tail of the migration flow are ready for nesting to the maximum extent. Bramblings belong to species that, upon arrival in the Subarctic, do not need photostimulation during the polar day. Males from the first wave of arrival, placed under short day conditions (14L : 10D), began to molt at the same time as the males that lived at the polar day in the enclosure, i.e., these birds do not need additional stay in the nesting area for puberty (Ryzhanovsky, 2001).

The main period of egg-laying in the control nests was in the second half of June and lasted 8–20 days, on average, 10.6 ± 1.5 ($n = 8$), and the laying season, from the first to the last egg, lasted 15–25 days, on average 17.6 ± 1.2 ($n = 8$). In the years 1978–1982, oviposition began after 9–26 days, on average, after 19.1 ± 2.4 days ($n = 6$) after a steady transition of the average daily temperature through 0°C, at 4.5–22.8°C, on average 10.9 ± 1.1°C ($n = 6$). It took 14 and 19 days from occupation of the nesting area by the male to the appearance of the first egg in the nest in the area. Out of 68 nests with full clutches, one had two eggs, one had three eggs, six had four eggs, 27 had five eggs, 28 had six eggs, and five had seven eggs. The mean clutch size is 5.39 ± 0.12. The clutch of bramblings is not significantly higher in Karelia, 5.59 ± 0.19 (Zimin, 1988).

Only the female incubates. Judging by the length of hatching in some nests, stable incubation may begin after laying the second or third egg when laying six eggs, but begins more often from the penultimate egg, but sometimes (Ryabitsev and Shubenkin, 1980) from the first. From the first egg to the hatching of the last chick, 17–21 days elapsed, on average, 18.5 ± 0.4 ($n = 6$), from the last egg to the first chick, 8–14 days, on average, 11.0 ± 0.7 ($n = 9$). The last period is the period of incubation itself; in fact, this is the period of incubation of the last egg in the conditions of the formed rhythm. Males feed the incubating females, but the latter are able to sit and feed the chicks alone. A female, having lost her male, incubated her clutch for 16 days from the last egg, then fed the chicks alone (Ryabitsev and Shubenkin, 1980; Ryabitsev et al., 1980). A female incubated a clutch with dead embryos for 20 days, until the termination of observations (Danilov et al., 1984).

The usual timing of hatching of chicks is from the first to the beginning of the second ten-day period of July. Hatching is often extended for a day ($n = 9$), in one nest it stretched for three days, and in another, for four days. The disturbed chicks jumped out of the nest on the 9th day, not being able to fly; the undisturbed ones left the nests after 10–12 days, on average, after 11.5 ± 0.4 ($n = 12$) after hatching. By the age of 12 days, the fledglings were able to fly away from the nest, depending on the height of its location, by 10–20 meters or more. The capability for active flight is acquired by the age of 18–20 days; the broods disintegrate when the fledglings reach 25–30 days of age.

In the nests monitored from the start of laying to the emergence of chicks, the total duration of the pair's nesting period was 27, 27, and 29 days. From the laying of the first egg in the season to the emergence of the last chick in the season, 39–61 days elapsed, on average, 47.4 ± 4.2 (five seasons of observations).

Brood migrations. Out of 35 brambling fledglings ringed in the nests, one was caught again, not far from the nest, at the age of 24 days. In early August, three birds 20–23 days old were caught with one net, apparently from the same brood. After 17 days, two of them were caught in nets not far from the place of the first capture. Since in small passerines, by the age of 30 days, broods usually break up and leave the nesting area in the process of dispersion, it can be assumed that some individuals in bramblings do not participate in dispersion. But the proportion of such birds is insignificant, because the brambling is the only songbird species in our area that was characterized by the predominance of adults in the second half of the summer during all years of trapping (Fig. 2). In the Sob valley, among the captured birds, the proportion of adults was 86%; at the Oktyabrskaya station, it was 81.1%. Undoubtedly, after the breakup of broods, the majority of young bramblings fly away from the forest–tundra. At the same time, the number of bramblings in the northern taiga of Western Siberia increases: from 53 individuals/km^2 in the first half of summer (landscape average) to 687 individuals/km^2 in the second half (Ravkin, 1978). Since the local population cannot provide such an increase, there is reason to believe that bramblings of a more northerly origin predominate here (Rogacheva et al., 1983); in the Yenisei forest–tundra, rapid migration of broods to the south was also noted.

But a small part of young bramblings remains in the forest–tundra zone, and possibly in the hatching area, almost until the start of migration. Over five years of trapping (1977–1981), 52 individuals were ringed in August, of which 11 (21.1%) were caught again: seven birds were in the control area from one to six days and four birds, 17–22 days. The behavior of these bramblings (which did not migrate from the nesting area) was typical for northern passerines: first, a short-term dispersion flight, then a long stop for post-juvenile molting (Ryzhanovsky, 1997).

Adult birds, judging by the repeated captures, after the breakup of the broods, remain in the area of the nesting territory until the start of departure. In particular, at the Oktyabrskaya station in 1978, in August–September, ten birds (seven males, three females) were caught out of 108 (71 males, 37 females) ringed at the catching site a month earlier, during nesting time.

Molt. In the annual cycle of bramblings, there is one molt that occurs in the nesting area: post-juvenile in young and post-nuptial in adults. The post-juvenile molt is partial; it covers the contour plumage and most of the wing coverts, as well as the down feathers on the aptery, and is divided into seven stages. In all bramblings caught in the middle stages of molting (n = 20) and reared in captivity under natural light (n = 4) molting of a part of (proximal) the greater, all the middle, and the lesser upper coverts of secondary feathers, the upper and lower coverts of the protagial fold, manus, and middle lower coverts of secondary feathers was recorded on the wing; most birds replaced the middle upper coverts of the primaries and the lower coverts of the tertiary primaries (Table 2). For the bramblings of the Kola Peninsula, Gaginskaya (1990)

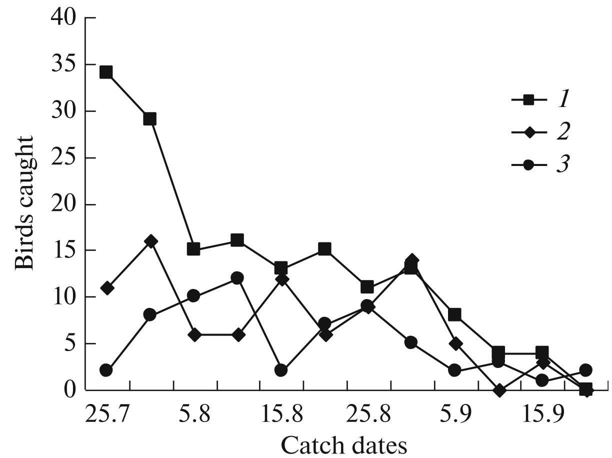

Fig. 2. The number of (*1*) males, (*2*) females, and (*3*) young bramblings caught with nets and traps at the Sob and Oktyabrskaya stations for a five-day period in late summer–autumn in the years 1976–1982.

indicates a molt of the middle upper coverts of the main primaries, which we did not find in birds caught in nature or in aviary birds. Possibly, the fullness of postjuvenile molting of bramblings in the western part of the range is greater than in the eastern part.

The completeness of molting in bramblings (n = 7), fed and overexposed until the beginning of September in the laboratory of the Oktyabrskaya hospital with a photoperiod of 24L: 0D was no more than in nature. In bramblings (n = 7), reared at 16L: 8D and overexposed with a shortening day (by 30 min over five days), the completeness of the molt was somewhat reduced: only the 17th–20th greater upper coverts of the secondaries were replaced as opposed the 12th–20th with a long day.

In Leningrad oblast, bramblings from early broods began to molt at the age of 30–35 days; and on the Kola Peninsula, at 20–25 days (Gaginskaya, 1990). Bramblings from the Lower Ob region, reared under different photoperiodic conditions, started breeding at different ages (Table 3). Differences are significant between the birds of the groups of short-day and long-day photoperiods; the age at which molting begins in bramblings depends on the length of the day (it is controlled by the photoperiod). But the age interval within which molting begins (14 days) is small compared, for example, with the chaffinch (*Fringilla coelebs*) (30 days) or common red-poll (42 days) (Noskov, 1975; Noskov and Smirnov, 1986; Ryzhanovsky and Ryabitsev, 2021).

Due to the significant completeness of molting, bramblings in captivity molted for quite a long time, at least 40 days with a short day and up to 70 days with a long day (Table 3). With a photoperiod of 24L : 0D (until the end of August, natural later) the molt lasted significantly longer than at 16L : 8D (reducing).

Table 2. Bray line scheme

Pterylia, departments pterylium	Post-juvenile molt stages							Post-brooding molt stages										
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	8	9	10	11
Head		□	■	■	■	□					□	□	■	■	■	■	■	■
Abdominal	□	■	■	■	■	■	■				□	■	■	■	■	■	■	■
Dorsal	□	□	■	■	■	■	□				□	■	■	■	■	■	■	■
Shoulder	□	□	■	■	■	□					□	■	■	■	■	■	■	□
Femoral		□	■	■	■	□				□	■	■	■	■	■	■	■	□
Calf		□	■	■	■	□					□	■	■	■	■	■	■	□
Anal		□	■	■	□							■	■	■	■	■	■	■
Steering										□	□	■	■	■	■	■	□	
UTC		□	■	■	■	□						■	■	■	■	■	■	□
LTC			□	■	■	□				□	■	■	■	■	■	■	■	□
1-st. Flywheels								■	■	■	■	■	■	■	■	■	■	□
2-nd. Flywheels													■	■	■	■	■	■
3-rd. Flywheels												□	■	■	■	■	□	
LUCPP								■	■	■	■	■	■	■	■	■	■	□
MUCP											□	□	■	■	□			
LaUCS			□	■	□						□	■	■	■	■	□		
MUCS			□	■	□						□	□	■	■	■	□	□	
LeUCS		□	■	□									■	■	■	■	■	□
UCPF	■	■	■	□									■	■	■	■		
CC															□	■		
FW															□	■	■	
CW		□	□	□										□	□	■		
UCB	□	□	□										□	■	■	■		
LCB	□	□	□	□									□	■	■	■		
LLCPP														■	■	■		
MLCPP														■	■	■		
LLCSP																■	■	
MLCSP			□	■	□									■	■	■		
LCTP				□	□										■	■		
Apteria		□	■	■									■	■	■	■		

Designations: ■, department feathers molt in all examined birds, □, department feathers molt in part of the examined birds. Full names of departments of pterylia: UTC, upper tail coverts; LTC, lower tail coverts; LUCPP, large upper coverts of primary primaries; MUCP, middle upper coverts of primaries; LaUCS, large upper coverts of secondaries; MUCS, middle upper coverts of secondaries; LeUCS lesser upper coverts of secondaries; UCPF, upper coverts of the protagial fold; CC, carpal covert; FW, fly wings; CW, covering wings; UCB, upper covering brushes; LCB, lower covering brushes; LLCPP, large lower coverts of primary primaries; MLCPP, middle lower coverts of primary primaries; LLCSP, large lower coverts of secondary primaries; MLCSP, middle lower coverts of secondary primaries; LCTP, lower coverts of tertiary primaries.

Table 3. Age of onset and duration of post-juvenile molting under different photoperiodic conditions

Photoperiod	Molting start age, days		Molting duration, days	
	N	Lim / $M \pm m$	N	Lim / $M \pm m$
SDP 16L : 8D reduced by 6 min/day to 12L : 12D	7	20–26 / 23.0 ± 0.9	7	40–48 / 43.2 ± 1.9
NPP 24L : 0D until mid-July declining later	4	22–27 / 22.6 ± 1.3	4	44–60 / 53.0 ± 3.9
LDP 24L : 0D until the end of August, natural later	7	25–34 / 28.6 ± 1.3	7	59–70 / 65.8 ± 1.8

Designations: SDP, short-day photoperiod; NPP, natural photoperiod; LDP, long-day photoperiod.

In the years 1977–1982, juvenile birds that had not begun to molt were caught between July 26–August 22 (n = 5), while this occurred for July 26–28 in 2018 (n = 4). In 1977–1982 we caught 20 molting bramblings between August 1–September 7 at molting stages 1–4; one individual was caught on September 20 at the 5th stage. We did not catch bramblings that were finishing or, moreover, that had finished molting. From the forest–tundra, young bramblings fly southward until the end of the molt. The regression equation (Pimm, 1976) compiled according to the average dates of molting gives the following results: beginning on August 9, end on September 28, and a duration of 51 days, which coincides with the course of molting of caged bramblings during a natural day. The season of post-juvenile molting (the timing of the meeting of young molting birds) in the bramblings of the Lower Ob region lasts about one and a half months, while the molting period of the population of northern birds is extended over 2.5–3 months and coincides with the migration period.

Completion of the postbrooding molt. The general sequence for changing plumage is given in Table 2 and does not differ from that of the birds of Leningrad oblast (Gaginskaya, 1990). A part of the bramblings, possibly significant, combines molting with reproduction. Two males and three females were caught from nests with 10- to 12-day-old chicks. One male had not begun to change plumage, but the rest of the birds were at the 2nd stage of molting. Bramblings beginning to molt were rarely caught at the 1st or 2nd stages. Most of the caught molting bramblings were at stages 4–7 and 10–11. Birds never lose their ability to fly, but at the 8th–9th stages, when the flight tips of the wing and most of the secondary flight feathers grow, the flying qualities undoubtedly decrease, so the birds are caught less often.

The post-brooding molting season begins in the first ten days of July, in the early spring years, perhaps even at the end of June (Rymkevich and Ryzhanovsky, 1987) and ends in the second ten days of September. Bramblings in their old plumage were captured until July 28, 1977, and August 4, 2018. The first molting birds were caught on July 17–28 (n = 4), but all of them had an advanced molt (stages 4–6); it had started 5–15 days earlier. The average calculated date (Pimm, 1976) of the end of the molt of males is September 7, and that of females is September 11; the average molt duration of males is 63 days, and that of females is 58 days. Judging by these data, the females begin to molt somewhat later than the males, which was not revealed during captures at the nests. They finish it a little later, and it goes at a faster pace. The latter is connected with the reaction to the shrinking day in August. Gaginskaya (1990) showed that, on the Kola Peninsula, bramblings, which start molting early, replaced their plumage in 70–75 days; late molting finishes in 55–60 days.

The period of entry into the post-brooding molt at the northern limit of the range, at the latitude of the Arctic Circle, is extended by almost a month. At the middle stages of molting, birds were caught at the same time. In particular, in 1978, at the 7th stage, males were caught for 25 days and females, for 31 days. Males kept since spring in an enclosure during a natural photoperiod (n = 7), i.e., those not participating in nesting, began to molt between June 25 and July 20, on average on July 10 and completed molting in the first half of September after 60–66 days, on average, after 63.4 ± 0.8 days. In this case, the timing almost completely coincided with the timing and rate of molting of males involved in reproduction.

Autumn migration. Departure began in mid-August, lasted over a month, until the third ten-day period of September. The dates of the last captures and encounters of bramblings on routes in the Polar Urals and in the floodplain of the Lower Ob are September 16–21. Adult birds that can be considered "native" (ringed in June–July) have ceased to be caught again and were included in the migration between August 16–September 17. In the same period, the number of unmarked bramblings, finishing the molt in a new plumage, increased on the site. Presumably, they nested to the north of our area; i.e., they were transitory. It is possible that the first stages of migration are made by flights with long stops. In particular, in 1978, in the period from August 29 to September 2, eight birds were ringed at the 10th–11th stages of molting on the site, and all of them were caught again after 2–16 days, some in new plumage. There are probably no sex-related differences in the timing of departure; females were caught until the end of the migration. Young bramblings, as mentioned above, leave the forest–tundra en masse in the first half of August. The rest fly away simultaneously with adult birds. In contrast to the spring migration, when bramblings fly in flocks, single species, or together with common redpolls, in the autumn, flocks of bramblings are very rare, and small groups predominate.

The autumn migratory state of breeding birds begins to form late. To determine the timing of the appearance of the southern direction of activity, adult birds caught in the third ten-day period of August were placed in cone cages (Emlen, S.T. and Emlen, J.T., 1966) ($n = 12$) and in the first ten-day period of September ($n = 10$). In August, a slight predominance of disturbance in the easterly and westerly directions was noted; in September, bramblings begin to choose the southern direction of activity (Ryzhanovsky, 2010). Fat accumulations in adult birds also form very late. Out of 28 bramblings caught in the third ten-day period of August, one individual had fat reserves estimated as "average"; in the first ten days of September, all 24 birds were skinny or low fat; in the second ten-day period of September, three birds (16.6%) out of 18 examined had average fat reserves.

In young bramblings, there are probably two periods of manifestation of the southern direction of activity: 1, short-term in most birds, at the initial stages of post-breeding migrations, during which the main part of the forest–tundra bramblings migrate to the taiga, and, 2, long for everyone, with the beginning of the formation of a migratory state. It is also interesting that, in the second ten-day period of August, during the time of migration to the taiga, among 12 bramblings caught, three had average fat reserves; i.e., another component of the migratory state was formed, but was probably also short-lived, before the development of intense molting.

Bramblings from our area fly to the southern part of Western Europe, as evidenced by the banding data. In 1979, in mid-July, a male with a Yugoslav ring was caught at the Oktyabrskaya station. Information about the specific location of tagging has not been received. A female brambling, ringed on August 12, 1980, at the Oktyabrskaya station was caught on November 5, 1980, in Italy: 45°45′ N, 12°35′ E. Since it should not fly away from our area before the beginning of September, that is, on the day of marking, it was at the 4th stage of molting; the bird spent less than two months on the entire migration route.

CONCLUSIONS

In Western Siberia, the northern border of the brambling range coincides with the northern border of floodplain forests; larch, willow, and alder forests in lake basins and mountain valleys. The nesting density remains high, locally 50–100 pairs/km^2, up to the border of almost continuous distribution of riparian forests and areas of floodplain light forests along the 67th parallel. Habitats suitable for nesting bramblings also exist to the north, for example, a forest island of considerable size in the Yadayakhodayakhi valley, but in the 1980s these birds nested there irregularly and at a low density. Most likely, the biotopic conditions do not directly limit the northward movement of the species.

Danilov (1966), in his analysis of the factors that determine the northern boundaries of the distribution of birds in the Subarctic, came to a conclusion about the decisive importance of phenological conditions; i.e., the summer part of the annual cycle of the species must fit into a certain limit of temperatures and seasonal phenomena. Bramblings arrive in the northern part of the range at positive daytime temperatures (close to 0°C), with the beginning of active snow melting in the forest, and fly away with the beginning of phenological autumn at positive, sometimes very high, temperatures. The departure of the last individuals ends after the fall of the leaves, but before the first snowfall. The total duration of stay of the brambling in the Lower Ob region, from the registration of the first spring bird to the registration of the last bird in the 1980s, is 102–137 days, on average, 112.2 ($n = 4$) days, and the average duration of the frost-free period at the latitude of Salekhard is 94 days. When comparing the average dates of the beginning of the mass arrival (the third ten-day period of May) and the completion of the mass departure (the first ten-day period of September), bramblings generally fit into the frost-free period of the forest–tundra. Taking into account the duration of the frost-free period at the latitude of the village of Tambei (Northern Yamal, 71° N) at 51 days (Orlova, 1962), its reduction is 7.8 days/1° geographic latitude, and in the valley of the Yadayahodayahi River, this period lasts about 85 days. The differences from the latitude of the Arctic Circle seem insignificant, but the view no longer fits into the frost-free period. The warming of the last ten-day periods should lead to an earlier arrival of the bramblings to the forest tundra, which is observed in some years, but the average dates for five years have not changed.

On the other hand, upon arriving in the forest–tundra with mature gonads, the birds lose their incentive to migrate and should not seek to expand their range at the expense of local light forests in the tundra zone. The photoperiodic conditions of the southern tundra (polar day for 1.5–2 months) do not stimulate further northward movement. The light regime of the taiga zone is sufficient for the start of nest building and egg laying for the brambling.

In my opinion, bramblings have no adaptations to the conditions of the Subarctic. This is a middle- and north-taiga species that develops the forest–tundra as it warms up and the light forests thicken.

ACKNOWLEDGMENTS

The author expresses his deep gratitude to the Director of the Arctic Station, Ural Branch, Russian Academy of Sciences, V.G. Shtro, for the kindly provided information about the dates of the arrival of bramblings in the vicinity of the city of Labytnangi.

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The author declares that he has no conflicts of interest.

Statement on the welfare of animals. This article does not contain any studies involving animals performed by the author.

REFERENCES

Blyumental', T.I. and Dol'nik, V.R., Geographical and intrapopulation differences in the timing of reproduction, molting and migration in some migratory passerine birds, in *Tr. Vsesoyuz. soveshch. po vnutrividovoi izmenchivosti nazemnykh pozvonochnykh i mikroevolyutsii* (Proc. All-Union Meet. on Intraspecific Variability of Terrestrial Vertebrates and Microevolution), Sverdlovsk, 1966, pp. 319—332.

Danilov, N.N., *Puti prisposoblenii nazemnykh pozvonochnykh zhivotnykh k usloviyam sushchestvovaniya v Subarktike* (Ways of Adaptation of Terrestrial Vertebrates to the Conditions of Existence in the Subarctic), vol. 2: *Ptitsy* (Birds), Sverdlovsk, 1966.

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

Emlen, S.T. and Emlen, J.T., A technique for recording migratory orientation of captive birds, *Auk*, 1966, vol. 83, pp. 361–367.

Gaginskaya, A.R., The brambling *Fringilla montifringilla* L., in *Lin'ka vorob'inykh ptits Severo-Zapada SSSR* (Moulting of Passerine Birds of the North-West of the USSR), Leningrad: Leningr. Gos. Univ., 1990, pp. 208–212.

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

Kucheruk, V.V., Kovalevskii, Yu.V., and Surbanos, A.G., Changes in the avifauna of South Yamal over the past 100 years, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 1975, vol. 80, no. 1, pp. 52–64.

Lindström, A., Breeding nomadism and site tenacity in the bramling, *Fringilla montifringilla, Ornis Fenn.*, 1987, vol. 64, no. 2, pp. 50–56.

Noskov, G.A., Finch (*Fringilla coelebs*) molt, *Zool. Zh.*, 1975, vol. 54, no. 3, pp. 413–425.

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

Noskov, G.A. and Smirnov, E.N., Some features of the photoperiodic control of the timing and completeness of the post-juvenile molting of the common redpoll, in *Aktual'nye problemy ornitologii* (Actual Problems of Ornithology), Moscow, 1986, pp. 69–75.

Orlova, V.V., *Klimat SSSR* (Climate of the USSR), issue 4: *Zapadnaya Sibir'* (Western Siberia), Leningrad: Gidrometeoizdat, 1962.

Paevskii, V.A., *Demograficheskaya struktura i populyatsionnaya dinamika pevchikh ptits* (Demographic Structure and Population Dynamics of Songbirds), St. Petersburg: KMK, 2008.

Paskhal'nyi, S.P., Dates of arrival of some bird species in the lower reaches of the Ob in 1970–2002, in *Mnogoletnyaya dinamika chislennosti ptits i mlekopitayushchikh v svyazi s global'nym izmeneniem klimata. Materialy mezhdunarodnogo simpoziuma* (Proc. Int. Symp. "Long-Term Dynamics of the Number of Birds and Mammals in Connection with Global Climate Change"), Kazan: Novoe znanie, 2002, pp. 151–156.

Pimm, S.L., Estimation of the duration of bird moult, *Condor*, 1976, vol. 78, no. 4, p. 550.

Ravkin, Yu.S., *Ptitsy lesnoi zony Priob'ya* (Birds of the Forest Zone of the Ob Region), Novosibirsk: Nauka, 1978.

Rogacheva, E.V., Ravkin, E.S., Syroechkovskii, E.E., and Kuznetsov, E.A., Fauna and population of birds of the Yenisei forest-tundra, in *Zhivotnyi mir eniseiskoi lesotundry i prirodnaya zonal'nost'* (Fauna of the Yenisei Forest-Tundra and Natural Zoning), Moscow: Nauka, 1983, pp. 14–47.

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.

Ryabitsev, V.K. and Shubenkin, V.P., On the duration of incubation in brambling, in *Inf. mat-ly IERiZh* (Information Materials of IERiZh), Sverdlovsk, 1980, pp. 80–81.

Ryabitsev, V.K., Golovatin, M.G., and Yakimkenko, V.V., Territoriality of passerines in the conditions of spring flood and experimental withdrawal of males, in *Ekologicheskie aspekty povedeniya zhivotnykh* (Ecological Aspects of Animal Behavior), Sverdlovsk, 1980, pp. 49–60.

Rymkevich, T.A. and Ryzhanovsky, V.N., Molting of birds in the Polar Urals, *Ornitologiya* (Ornithology), Moscow: *Mosk. Univ.*, 1987, vol. 22, pp. 84–95.

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

Ryzhanovsky, V.N., Breeding season as part of the annual cycle of Subarctic passerines, in *Gnezdovaya zhizn' ptits*

(Nesting Life of Birds), Perm: Perm. Gos. Pedagog. Inst., 2001, pp. 3–22.

Ryzhanovsky, V.N., Body weight and fat reserves of passerines of the Lower Ob region, *Russ. Ornitol. Zh.*, 2004, no. 13 (271), pp. 799–812.

Ryzhanovsky, V.N., Nesting attempts of some species of finches on the spring migration routes, *Russ. Ornitol. Zh.*, 2008, no. 17 (418), pp. 731–733.

Ryzhanovsky, V.N., Formation of the direction of autumn migration in some passerines of the Lower Ob region, *Russ. Ornitol. Zh.*, 2010, no. 19 (564), pp. 671–680.

Ryzhanovsky, V.N. and Paskhal'nyi, S.P., Dynamics of the bird population of the Lower Ob in connection with climate warming, *Nauchn. Vestn. Yamalo-Nenets. Avtonom. Okruga*, Salekhard, 2007, no. 6 (50), part 2, pp. 58–74.

Ryzhanovsky, V.N. and Ryabitsev, V.K., Biology and ecology of the redpoll (*Acanthis flammea* sensu lato, Passeriformes, Fringillidae) on Yamal Peninsula and in the Near-Ob Forested Tundra, *Biol. Bull.* (Moscow), 2021, vol. 48, no. 8, pp. 1347–1357.

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

Shutov, S.V., Nesting density of common passerine species (Passeriformes) in the Subpolar Urals and some patterns of its spatial variation in the floodplains of the South Subarctic, *Zool. Zh.*, 1990, vol. 69, no. 5, pp. 93–98.

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

Zimin, V.B., *Ekologiya vorob'inykh ptits Severo-Zapada SSSR* (Ecology of Passerines in the North-West of the USSR), Leningrad: Nauka, 1988.