

Post-Juvenile Molt of the Brambling (*Fringilla montifringilla*, Passeriformes, Fringillidae): A Study of Four Places

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Abstract—The duration of molt and its different stages in young bramblings and variability under the influence of photoperiodic conditions are considered. The timing and duration of molt seasons in different places of the distribution area are also investigated, and their determining factors are clarified. The molt process is divided into seven stages. The signs of the stages are the beginning or end of feather replacement in the selected tracts of the feather coat. An analysis of the experimental data revealed the influence of photoperiodic conditions on the duration of the molt of an individual. Under photoperiods corresponding to early molt timing, molt duration averaged 62.0 days, compared to 52.3 days under the conditions of late molt timing. The molt duration is shown to drop as a result of a decrease in the duration of the beginning stages. Data derived from repeated catches in nature confirmed the results of the experiment. A negative relationship was found between the timing of the capture of bramblings and the duration of their intervals between stages 2 and 3 and 3 and 4. A comparison of the duration and timing of the seasons of post-juvenile molt at four different places of the distribution area showed their great geographic variability. The duration of the season is increased in the following sequence: the Lower Ob region (66°40' N, 66°40' E), the White Sea region (67°06' N, 32°41' E), the Middle Ob region (59°58' N, 74°22' E), and the Ladoga region (60°41' N, 32°57' E), amounting to 39, 64, 92, 116 days, respectively. In almost the same sequence, the dates of these seasons reliably shift from early to late. The median catch dates for molting birds are August 24 in the Lower Ob region, August 28 in the White Sea region, September 1 in the Ladoga region, and September 10 in the Middle Ob region. At an early start of the molt season in the Ladoga region (July 2), its end turned out to be one of the latest (October 25), and the duration is twice as long as that of an individual molt. In the Lower Ob, at a late start of the season (August 1), it ends earlier than at other locations of the study area (September 8), and its duration is almost half as long as the molt of an individual. An analysis of the number of birds with different stages and a comparison of the timing of registration of successive stages at each research location with the duration of inter-stage intervals in molting individuals have allowed us to come to the following conclusion. During the post-juvenile molt season, the Lower Ob region is inhabited mainly by local bramblings with the beginning molt stages. They fly away from this subarctic area before the onset of intense feather replacement. In the study area of the White Sea region, the molt season is dominated by birds that appeared as a result of post-fledging (juvenile) migration. They have middle molt stages. In the Ladoga and Middle Ob regions, both local birds and bramblings from remote territories are recorded. Among the latter, there are birds that live during middle molt stages, but individuals with the last molt stages, which follow in transit during the autumn passage, predominate. This determines the longer duration and the later dates of the molt seasons in the Ladoga and Middle Ob regions.

Keywords: molt duration, photoperiodic control, molt season, geographic variability

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INTRODUCTION

The feather coat of birds requires periodic renewal. Molting, which involves complete or partial replacement of the plumage, occurs once or twice a year in most species. It is determined by specific hormonal

and physiological conditions and occupies a specific place in the annual cycle of seasonal events (Voitkevich, 1962; Stresemann, E. and Stresemann, V., 1966; Jenni and Winkler, 1994; Newton, 2009). Although molt, like reproduction or migration, requires signifi-



Fig. 1. Research sites.

cant energy expenditure, it is the most flexible process in terms of intraseasonal and geographic variability. Changes in the timing and duration of molt allow birds to adjust their annual cycle to local environmental conditions (Noskov et al., 1999). Despite the clearly adaptive nature of molt variability, it has received far less attention than other seasonal events of the annual cycle, such as the reproduction or migration. This is especially true for molt during the first year of life.

In most passerines of high and temperate latitudes, the first, post-juvenile molt of young birds is partial, without the replacement of remiges. There is no generally accepted method for recording a partial molt. This largely explains the relatively poor study of post-juvenile molt. One method for recording partial molt is to divide it into distinct phases—molt stages (Noskov and Gaginskaya, 1972; Bursky, 2015). According to Noskov and Gaginskaya's method, partial molt stages are distinguished by the time selected tracts of the feather coat enter and exit the molt. Thanks to the simplicity of the technique, which allows for rapid determination of the stage of plumage replacement during bird examination, extensive data on the molt of passerine birds has been collected in the Ladoga region (Rymkevich et al., 1990), the Lower and Middle Ob region (Ryzhanovskii, 1997; Strel'nikov, 2019), the White Sea region (Panov, 2011; Shutova, oral communication), and other areas. The accumulated long-term data make it possible to study many aspects of the adaptive variability of molt in different bird species, including variability in its timing and duration. Comparison of these data with data on migratory mobility during molt also allows us to answer the question of whether local birds or birds from different populations are present during the molt season at a given point in its range.

The object of our study was the post-juvenile molt of the brambling (*Fringilla montifringilla* Linnaeus 1758). The breeding range of the brambling extends from Scandinavia to Kamchatka, in places reaching the 71st parallel in the north and the 52nd parallel in the south. To date, data on the post-juvenile molt of the finch have been accumulated at four geographically distant points of the range (Fig. 1). Of these, the Oktyabrskii station in the Lower Ob region (NE research point) with the Luvenga station in the White Sea region (NW), as well as the Negus'yakhskii station in the Middle Ob region (SE) with the Ladoga ornithological station (LOS) in the Ladoga region (SW), are located at the same latitude and are separated from each other by 1500 and 2200 km, respectively. At the same time, the NE and SE, as well as the NW and SW, points are similar in longitude and are separated from each other by about 700 km. This arrangement of the study areas facilitates the comparison of molt processes in nature to study the spatial variability and characteristics of molt timing at the northern limit of the range (at the latitude of the Arctic Circle) compared to more temperate latitudes. The results of work with the brambling in the lower reaches of the Ob River and photoperiod experiments with juveniles of this species have been partially published (Ryzhanovskii, 1997, 2008, 2023). The dependence of the molt process of the Lower Ob bramblings on photoperiodic conditions of maintenance is shown.

The main objectives of this study are to determine the individual duration of plumage change, including individual molt stages, and the relationship of these indicators with the photoperiod; the timing and duration of molt seasons at different points within the breeding range; and the factors influencing these indicators.

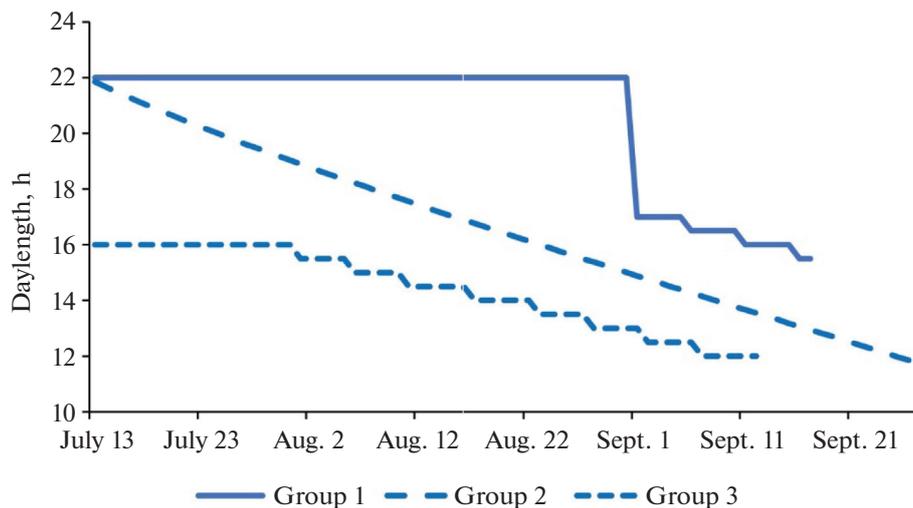


Fig. 2. Photoperiodic conditions in three experimental groups.

MATERIALS AND METHODS

This paper analyzes data obtained in nature and during laboratory keeping of birds under different photoperiodic conditions.

When examining the plumage of molt birds, the molt stage was determined as one of eight at the Luvenga station and LOS (Rymkevich et al., 1990) and one of seven at the Oktyabrskii station (Ryzhanovskii, 2023). When identifying eight stages, the first and second ones corresponded to stage 1 when recording seven stages. Subsequent stages had essentially the same characteristics. To facilitate comparison of data obtained in different study areas, the first two stages of birds from Luvenga and LOS were combined into one. At the Negus'yakhskskii station, the feather molt of each individual was described using a method that allowed for recording the proportions of old, growing, and new feathers in each tract of the feather coat (Rymkevich et al., 1987). Based on these descriptions, one of the seven stages was determined.

To analyze the individual duration of the molt, we used data from repeated captures in the wild and the results of a photoperiod experiment. For the latter, bramblings were taken from nests in the vicinity of the Oktyabrskii station. From the nestlings fed from the age of 10–14 days, three groups were formed, kept under different photoperiodic conditions (Fig. 2). Bramblings of group 1 (hatching June 28 through July 15, $n = 7$), long-day photoperiods (LDPP), lived in natural light until mid-July. The daylength, excluding twilight, had decreased to 22 h by this time. The birds were kept in these conditions until the end of August, after which the daylength was reduced to 17 h and then reduced by 30 min once every five days. By the end of the experiment, the daylength in group 1 was 15.5 h. Group 2 (hatching July 5–13, $n = 4$) was kept in an

aviary with natural photoperiod of 66.5° N (NDPP). Daylength decreased from 24 to 12 h during the experiment. After daylength reached 16 h at the beginning of the 3rd ten-day period of August, it decreased by an average of 7.3 min daily. Group 3, short-day photoperiod (SDPP), was formed in mid-July. Birds in this group (hatching June 27–July 4, $n = 7$) were immediately placed under 16-h daylength and lived under this PP until the beginning of August. Daylength then decreased by 30 min every five days. Birds from all three groups were kept until the 20th of September. The molt stage of bramblings in the experiment, as well as in free-living birds, was recorded. Each individual was examined during molt from seven to 12 times.

To analyze the duration of molt and/or its individual stages, both in the wild and in the laboratory, two methodological approaches were used. For both laboratory-raised birds and those in the wild that were examined more than twice during molt, a linear regression equation was used to determine the individual duration of molt and its separate stage (Fig. 3). By substituting the values for two consecutive stages into the equation, the average duration of the stage was found by subtracting the calendar dates corresponding to these stages. The total molt duration was then determined by multiplying this value by the total number of stages.

Regression analysis fails to detect differences in the duration of separate stages of individual molt, which may occur under different environmental conditions. Therefore, another methodological approach was to use the interstage molt interval. This indicator allows us to assess the durations of separate molt stages and identify which of them influence the overall duration of plumage change. We defined the interstage interval as the time between recordings of two adjacent molt

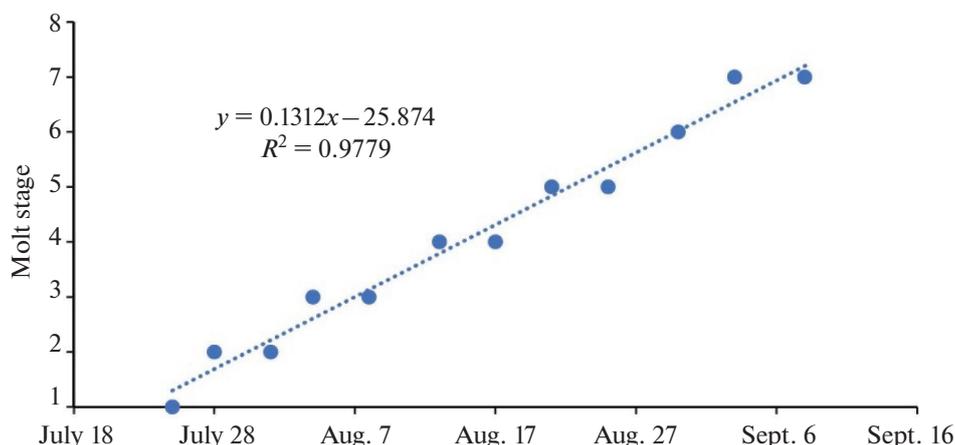


Fig. 3. Scatter plot of individual molt with a linear trend using the example of one of the bramblings from the experimental group of short-day photoperiods.

stages. During repeated surveys of a molt bird, the value of this indicator varies from zero to the combined duration of the two stages. With a normal distribution in the sample, the mean value of this indicator will be the interval between the middle of one stage and the middle of the following stage. Comparison of the interstage intervals of pairs of stages 1 and 2, 2 and 3, and other pairs of adjacent stages was used in the experiment to compare the duration of different molt stages in the same group and to compare the duration of the same stage in different groups. Using data from captured bird, the interstage interval was used to analyze the relationship between its duration and the date of registration of the first of two adjacent stages.

The molt season was defined as the period during which molt birds were present in a given area. The total molt season was defined as the time interval during which molt birds were recorded over all observation years. In addition to locally resident birds, the study area may also contain young bramblings that have begun molt and are undergoing post-fledgling migration (juvenile migration), newly emerged juveniles settling in for the period of intensive plumage change,

and first-year birds completing molt but already engaged in post-molt migration to their wintering grounds (migration period terminology according to Noskov, 2016).

The term “population” was used to refer to birds that were born in the same area.

Statistical analysis of the data was performed using the Statistica 10 program.

RESULTS

Individual duration of molt. The duration of molt and its separate stage, calculated in three experimental groups using individual linear regression equations, are presented in Table 1. In groups 1 and 2, the molt duration was statistically significantly longer than in group 3 ($p < 0.05$, t-test). Birds of group 3 were transferred to a photoperiod (16L : 8D) corresponding to the latest dates of birth while still nestlings. At the same time, no significant differences in molt duration were found between groups 1 and 2 ($p > 0.05$, t-test). In group 1, molt occurred with a reduction in the dura-

Table 1. Duration (D) of an separate stage and the entire molt of bramblings according to individual linear regression equations under experimental conditions and in nature (repeated captures)

Sample	<i>n</i>	Conditions	R^2	D stage/D molt, days	
				M	SD
Experiment					
Group 1	7	LDPP	0.94–0.98	9.4/65.9	1.89/13.23
Group 2	4	NDPP	0.96–0.98	8.9/62.0	1.13/7.92
Group 3	7	SDPP	0.94–0.9	7.5/52.3	0.54/3.81
Examined in nature	25	NDPP	0.90–1.00	10.4/72.9	4.39/30.78

n is the number of individuals. Here and in Table 2, LDP means long-day photoperiods, SDPP stands for short-day photoperiods, and NDPP is photoperiods with naturally varying daylength.

Table 2. Time intervals (days) between the dates of recording two consecutive stages of molt of bramblings in experimental conditions and in nature (repeated captures)

Interstage interval	Group 1 – LDPP			Group 2 – NDPP			Group 3 – SDPP			Catches in nature		
	<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD	<i>n</i>	M	SD
1_2	17	9.3	4.07	14	8.5	5.03	11	3.9	2.12	22	7.3	3.44
2_3	14	9.4	4.45	11	11.5	5.80	17	6.8	2.36	87	9.1	4.90
3_4	16	9.3	4.67	10	12.8	4.73	23	8.6	3.45	152	10.7	5.36
4_5	13	9.0	3.14	5	—	—	22	8.5	3.29	13	8.6	6.24
5_6	5	—	—	4	—	—	13	7.9	2.92	1	—	—
6_7	0	—	—	3	—	—	11	7.5	3.36	0	—	—

n is the number of interstage interval values. M and SD are defined for $n \geq 10$.

tion of daylength from 24 to 15.5 h, while in group 2 the daylength was reduced from 24 to 12 h.

Thus, the overall duration of molt was shorter in experimental group 3. In this group, the photoperiod conditions simulated those under which young bramblings from late broods undergo plumage change. However, the difference in average molt duration in this group, compared to the groups with a longer day, was only ten days, meaning the reduction in the duration of the entire process of plumage change did not exceed 15%.

To determine the molt parameters in nature using the regression equation, we analyzed data only for those individuals that were described during molt at least three times and the coefficient of determination of the linear equation, as in the experiment, was not less than 0.9. The average duration of the stage was 10.4 days, and the entire molt lasted 72.9 days (Table 1). Differences in the duration of molt between natural and experimental data were not statistically significant (Mann–Whitney U-test: $p > 0.05$). At the same time, the large value of the standard deviation indicates that, when using the linear regression equation to estimate individual duration of molt, even with 3–5 repeated captures, a significant random error occurs.

Duration of interstage molt intervals in an individual.

To determine the shortening of which molt stages leads to a decrease in the overall molt duration, we compared different stages within each group. For this purpose, we determined the duration of interstage intervals in each experimental group based on the difference in the dates of recording adjacent stages. Only those intervals with at least ten values were compared (Table 2). According to the Smirnov–Kolmogorov criterion, the distributions of time intervals did not differ significantly from normal. It was possible to compare the duration of all interstage intervals with each other only for group 3. The time interval between stages 1 and 2 (interstage interval 1–2) averaged 3.9 days and was significantly shorter than all other intervals ($p < 0.01$ and $p < 0.001$; t-test). Differences

between the remaining intervals were not statistically significant. For groups 1 and 2, we did not have sufficient data for all intervals: in group 1 due to the fact that molt was not yet complete by the end of the experiment, and in group 2 due to the small number of individuals (Table 2). In group 1, all four intervals available for comparison were of virtually the same duration. In group 2, the mean interval values differed by 1–4 days. However, the differences were not statistically significant (t-test: $p > 0.05$).

Thus, with long-day photoperiods, the molt stages we identified turned out to be equal in length; with short-day photoperiods, the initial stage was shorter than all the other stages.

When comparing the same interstage intervals of different groups, no significant differences were found between groups 1 and 2 for any interval. In group 1, compared with group 3, the interstage intervals 1_2 ($p < 0.001$, t-test) and 2_3 ($p < 0.05$, t-test) were significantly longer; in group 2, compared with group 3, the intervals 1_2 ($p < 0.01$, t-test), 2_3 ($p < 0.01$, t-test), and 3_4 ($p < 0.01$, t-test) were. These differences confirm that the photoperiodic response to short-day photoperiods shortens the duration of the initial stages of molt, thereby reducing its overall duration.

The large number of recaptures at the Luvenga station allowed us to verify the experimental results with observations in the wild. To determine the duration of interstage intervals, we used all time intervals between the dates of recording adjacent stages, including birds captured only twice during molt. Sufficient data for analysis were available only for the first four interstage intervals, as only one bird was captured at interval 5_6 and there were no captures of bramblings at interval 6_7 (Table 2). The shortest interstage interval was 1_2, and the longest was 3_4. These intervals differed statistically significantly in duration ($p = 0.007$, Mann–Whitney U-test). These differences suggest that, at least in some bramblings molt in the circumpolar

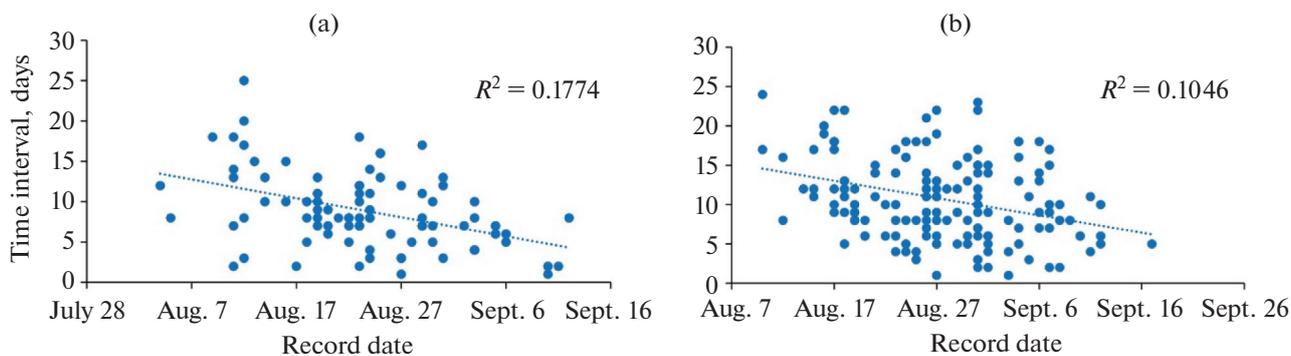


Fig. 4. The relationship between the duration of the time interval between recordings of successive molt stages and the date of the first of two surveys, according to data from repeated captures at the Luvenga station: (a) stages 2 and 3; (b) stages 3 and 4.

region, the photoperiodic response shortens the duration of the initial molt stage.

Having a relatively large amount of data for interstage intervals 2_3 and 3_4, we found an inverse relationship between the date of the first examination in these pairs and the duration of the interval (Fig. 4). The Spearman rank correlation coefficient between the date of registration of stage 2 and interval 2_3 was -0.38 ($p < 0.05$), and that between the date of registration of stage 3 and interval 3_4 was -0.29 ($p < 0.01$). This means that, in birds molt at later calendar dates, the duration of the stages of the first half of the molt is reduced.

Thus, a comparison of interstage intervals in the experiment revealed a reduction in the duration of the initial stages in young bramblings under the influence of short-day photoperiods. It also showed that, without the stimulating influence of such photoperiodic conditions, at least the stages of the first half of the molt are the longest and of equal duration.

An analysis of the relationship between the duration of interstage intervals and the date of the first examination, based on data from repeated captures in the wild, indirectly confirms photoperiod control of the post-juvenile molt of the brambling. In addition to the experimental data, it showed that the entire first half of the molt is stimulated by short-day photoperiods. This leads to a reduction in the duration of the entire molt and its completion at an earlier age.

Molt season. In the Lower Ob region, young bramblings were captured in small numbers. In the period 1977–1982, only 50 birds were captured. Of these, 19 individuals (43.7%) had not yet started molt. Nonmolt birds were captured between July 25 and August 21. The proportion of molt bramblings was insignificant until mid-August (Fig. 5a). Molt birds were captured between August 1 and September 8, over a period of 39 days. The median date of their capture was August 24. Birds replacing plumage were mainly at stages 1–4 of molt. There were very few bramblings at stages 5 and 6.

Birds at the last, 7th, stage, as well as those that had molted, were not captured at all (Fig. 6a). The bramblings at stage 1 were caught between August 1 and August 23; those at stage 2, between August 12 and August 23; at stage 3, between August 5 and September 7; at stage 4, between August 24 and September 2; at stage 5, between August 19 and August 29; and at stage 6, on September 8.

At the Luvenga station in the White Sea region, molt bramblings were captured between July 28 and September 29, a period of 64 days. The proportion of molt birds captured at the end of July and the first ten days of August was only 3.0%, and 2.1% in the last five days of September. The peak in the number of molt birds occurred in the last five days of August (Fig. 5b). The median date of their capture was August 28. Birds that had not yet begun to molt constituted less than 1% of those captured. Their proportion varied from 0 to 4.5% across the years. The last individuals not yet molt were captured between July 31 and August 28 in different years. Only 2% of fully molted birds were captured. Their proportion varied from 0 to 12.5% across the years. The first molted bramblings appeared in the catches between August 22 and September 19.

Among the molt bramblings, the largest number of birds were at stage 4 (32%), and together with stages 2 and 3, they accounted for 75%. During this time, bramblings undergo renewal in most tracts of their feather coat. Birds ringed at stages 2–4 were often recaptured there. Of the 7629 molt bramblings, 5% remained at the ringing site for at least five days. Of these, 76% were ringed at the height of the molt, from stage 2 to stage 4 inclusive. Birds at stages 1, 5, and 6 constituted the smallest proportion of the captures (Fig. 6b). There were more bramblings at stage 7 than at the two previous stages, but they accounted for only 11% of the molt birds.

The timing of capture of molt bramblings varied across years. The median date ranged within 22 days, from August 19 to September 9. The earliest molt sea-

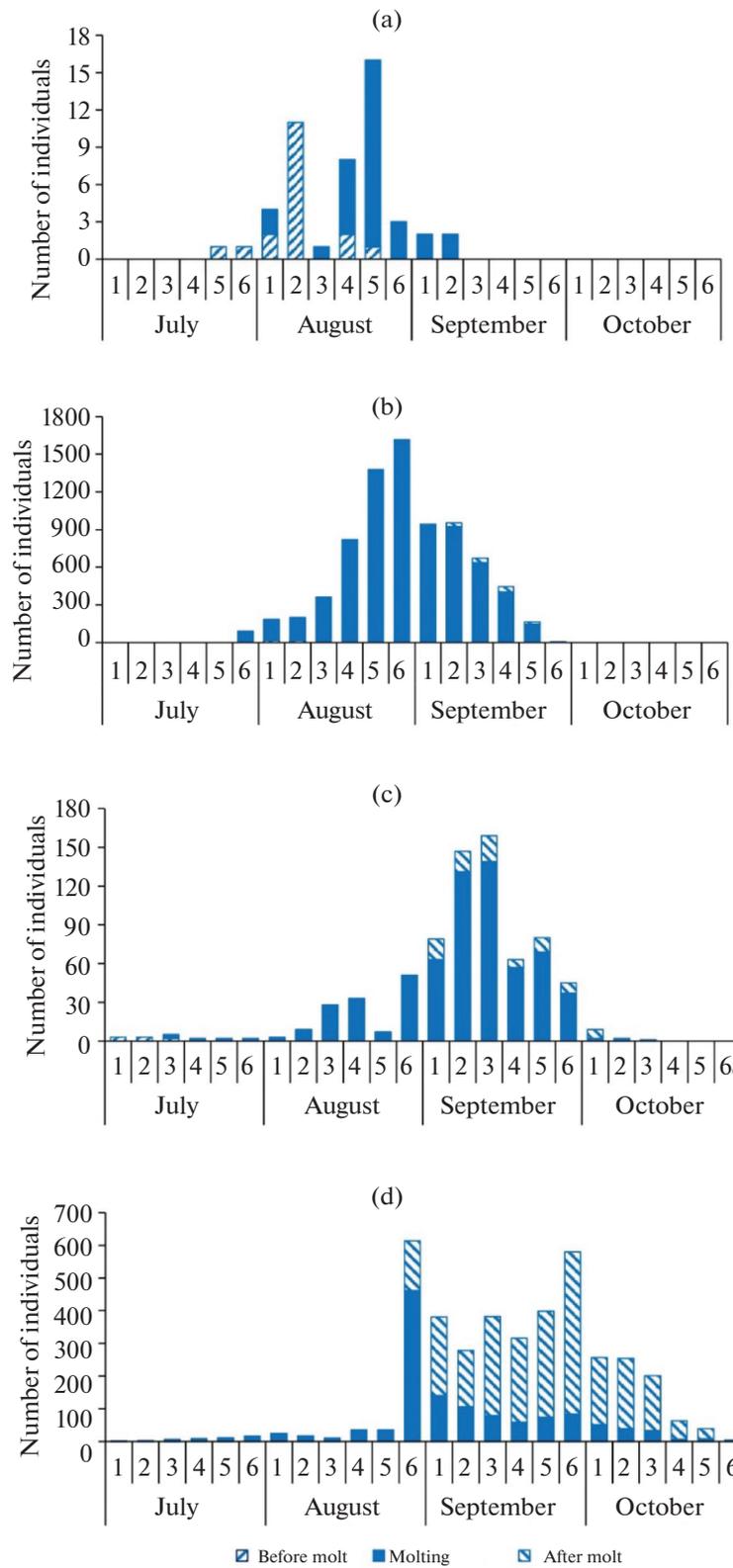


Fig. 5. Dynamics of the number of first-year bramblings in five-day catches in different territories: (a) Lower Ob region; (b) White Sea region; (c) Middle Ob region; (d) Ladoga region.

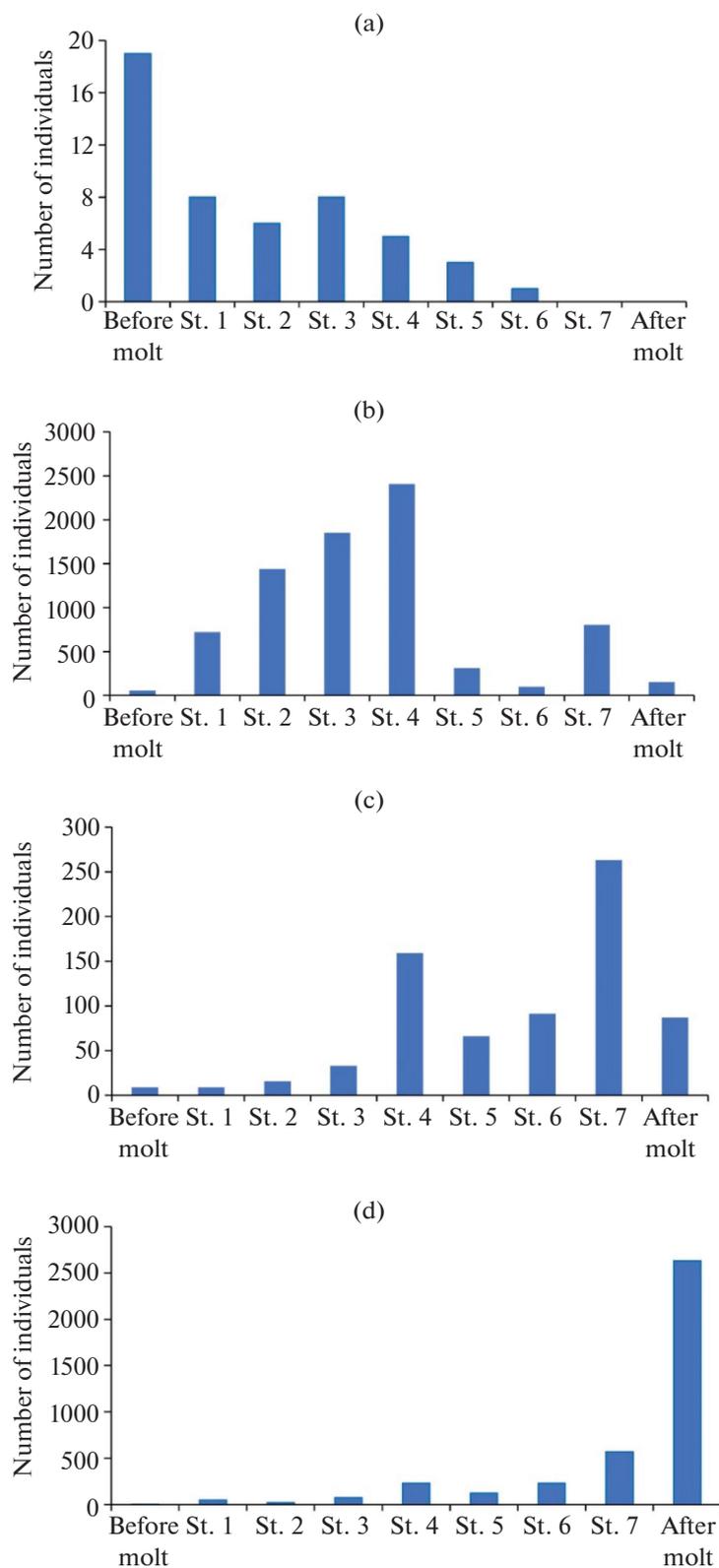


Fig. 6. The number of first-year bramblings with different plumage conditions, captured in different areas: (a) Lower Ob region; (b) White Sea region; (c) Middle Ob region; (d) Ladoga region.

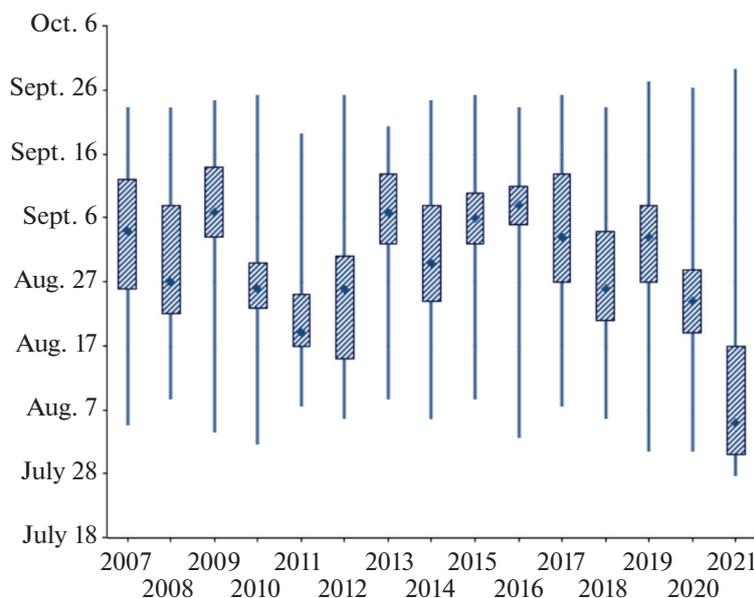


Fig. 7. Interannual variability in the timing of the post-juvenile molt season for bramblings in the White Sea region. Here and in Fig. 8, the diamond represents the median, the rectangle represents the interval between 25 and 75%, and the line represents the interval between the first and last dates.

sons occurred in 2010, 2011, 2020, and 2021. These years differed significantly from 2009, 2013, 2015, and 2016 (Fig. 7; $p < 0.001$, Mann–Whitney U-test).

In the White Sea region, the timing of successive molt stages varied ($p < 0.01$, Mann–Whitney U-test), with the exception of stages 5 and 6 ($p > 0.05$, Mann–Whitney U-test). The interval between medians for most of them did not exceed six days (Table 3), and averaged 3.3 days. Consequently, it was significantly shorter than the interstage molt interval for the individual. Apparently, not only local molt birds were captured in Luvenga; there was also an influx of birds in more advanced molt stages, arriving here from other areas.

In the Middle Ob region, molt young bramblings were recorded between July 11 and October 10, while capture at the Negus'yakhskii station began in early July and in some years ended in late October–early November. The duration of the total molt season was 92 days. The peak in the number of molt birds occurred on the 3rd five-day period of September (Fig. 5c), the median date of the total molt season was September 10. Only nine (1.2%) bramblings that had not started molt were caught. All of them were captured during July. Completely molted birds accounted for 11.9%. They were recorded between August 31 and October 15. The number of molt birds in the captures gradually increased from stage 1 to stage 4. Then it noticeably decreased from stage 4 to stage 5 and again began to increase towards the last, 7th stage (Fig. 6c).

Table 3. Timing of recording different stages of molt (Me) in bramblings in different territories

Molt stage	Middle Ob region		<i>p</i>	White Sea region		<i>p</i>	Ladoga region	
	<i>n</i>	Me		<i>n</i>	Me		<i>n</i>	Me
1	7	26.07	0.012	720	20.08	0.000	49	31.07
2	16	13.08	0.000	1441	22.08	0.000	22	31.07
3	33	16.08	0.000	1850	27.08	0.880	76	29.08
4	159	4.09	0.828	2406	2.09	0.000	230	31.08
5	66	11.09	0.000	312	5.09	0.091	126	31.08
6	91	11.09	0.000	97	7.09	0.052	230	1.09
7	263	13.09	0.000	803	10.09	0.000	569	13.09

n is the number of individuals. The significance of differences was assessed using the Mann–Whitney U-test. Statistically significant differences are highlighted in bold.

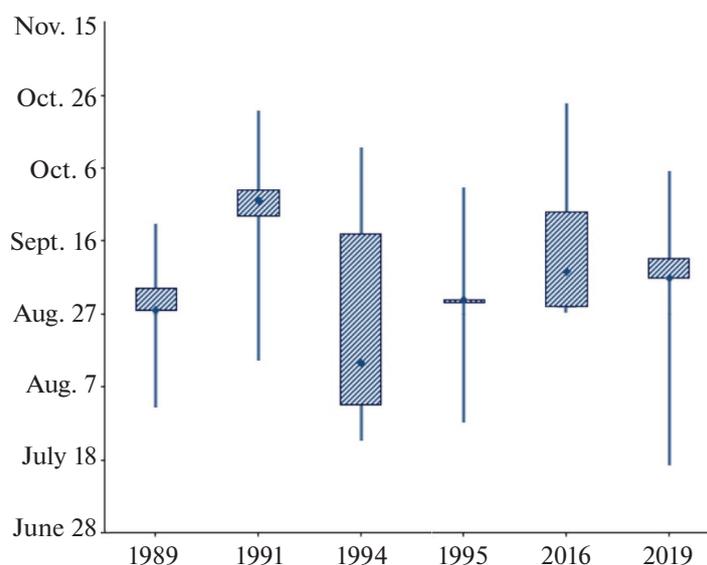


Fig. 8. Interannual variability of the timing of the post-juvenile molt season of bramblings in the Ladoga region (years with the number of birds caught molt >30).

Among the molt bramblings, the largest number of birds were at stage 7 (41.3%), and together with stages 5 and 6 and those that had molted, they constituted 59% of all those caught. Bramblings at the initial and middle stages were caught until the end of September. Birds at the last three stages, probably already involved in the post-molt migration, were caught from mid-August. Statistically significant differences in timing were found only between stages 3 and 4, 4 and 5, and 6 and 7 ($p < 0.05$, Mann–Whitney U-test). The median dates of recording successive molt stages are presented in Table 3. The interval between the medians of stages 3 and 4 turned out to be much greater than the average interstage interval of these molt stages of the individual. This suggests that bramblings caught at these molt stages are of different origins.

At LOS, bird captures are conducted daily from spring to late autumn. The first molt bird during this period was recorded on July 2; the last, on October 25. The duration of the total molt season was 116 days. The median date was September 1. Six birds that had not yet started molt were captured between July 1 and August 4. Fully molted bramblings were captured starting on August 20 (Fig. 6d) and accounted for 67% of the captures. The latest capture of a molted bird occurred on October 29. Years varied significantly in the number of molt bramblings captured, as well as in the first and median dates of their captures. From one to 420 molt bramblings were captured at LOS annually. In years when at least 30 individuals were caught ($n = 9$), the first capture varied between July 10 and August 29, and the median dates was within 30 days, between August 13 and September 11. Moreover, the molt seasons in 1989 and 1995 were significantly ear-

lier than in 1991 and 2019 (Fig. 8; $p < 0.001$, Mann–Whitney U-test). Other differences between years were not significant.

In the Ladoga region, the majority of molt bramblings were birds from stage 7 (44%; Fig. 6d), while stages 2–4 accounted for only 25% of captures, and stages 5 and 6 accounted for about the same number—27%. Only in 18 of the 34 years of the study were bramblings recorded from stages 1 and 2, which undoubtedly were born in the Ladoga region. Among bramblings caught at LOS, differences were found between the timing of passing stages 2 and 3, as well as stages 6 and 7 ($p < 0.001$, Mann–Whitney U-test). The median dates of captures at different stages of the molt are presented in Table 3. The median dates of stages 1 and 2 coincided. The difference in the median dates of successive stages 3 and 4, 4 and 5, 5 and 6 did not exceed two days; i.e., it was much shorter than the average interstage intervals for the individual. At the same time, the difference in the median dates of stages 2 and 3, and 6 and 7, was significantly greater than the interstage intervals of the individual molt, amounting to 29 and 12 days, respectively. All this indicates different origins of the birds captured during the molt season in the Lake Ladoga region.

Having compared the total post-juvenile molt seasons of bramblings in the Lower Ob region (NE), White Sea region (NW), Middle Ob region (SE), and Ladoga region (SW), we obtained the following results. The timing of the seasons differed significantly between all areas ($p < 0.001$, Mann–Whitney U-test). They were earliest in the Lower Ob region (Me = 24.08), and latest in Ladoga region (1.09) and Middle Ob region (Me = 10.09). The White Sea region (Me =

28.08) occupied an intermediate position in terms of the timing of the molt season. At the same time, the beginning of the seasons in Ladoga region (July 2) and in the Middle Ob region (July 11) was significantly earlier than in White Sea region (July 27) and in the Lower Ob region (August 1).

To determine at what stage the early-onset molt seasons in the Ladoga (SW) and Middle Ob (SE) regions become late, while the late-onset seasons in the White Sea (NW) and Lower Ob (NE) regions, on the contrary, become early, we compared the timing of each molt stage in different observation areas. The seasons in the White Sea and Lower Ob regions did not differ significantly in the timing of the first four molt stages. Young bramblings disappear from the Lower Ob region after stage 4. As a result, the molt season there ends at the earliest time. In the remaining areas, birds were recorded at all seven molt stages. In the Middle Ob region, while the first three molt stages were significantly earlier than in the White Sea region, the timing of subsequent stages became later, starting from stage 5. In the Ladoga region, also with earlier dates of the initial stages of molt, the change of the plumage became later than in the White Sea region, only towards the last stage (Table 3).

To compare the timing of molt seasons in the same years, we selected years in which at least 30 molt birds were captured: four years for the Luvenga station and LOS and three years for LOS and the Negus'yakhskii station. In 2007, 2010, and 2019, the timing of molt seasons in the Ladoga region at LOS was later than in the White Sea region at the Luvenga station ($p < 0.001$, Mann–Whitney U-test), with the medians differing by 19, 6, and three days, respectively. In 2016, the differences between the medians were one day and were not statistically significant. In the Middle Ob region, at the Negus'yakhskii station, the molt season dates were later than in the Ladoga region at LOS in 1989 and 1994 ($p < 0.001$, Mann–Whitney U-test), differing in medians by 11 and 35 days, respectively. However, in 1991, with the same level of significance, the molt season in the Middle Ob region was earlier than in the Ladoga region, with a difference in medians of 19 days. This result is undoubtedly partly due to differences in the molt progress of the captured birds. Thus, at LOS, the median stage in 1991 was stage 7, and in 1994, stage 3. However, the birds caught at LOS did not differ in the advancement of molt in 1989 and 1991 from those captured at the Negus'yakhskii station. Therefore, the differences in the timing of these seasons indicate that the birds began to change their plumage at different times and, obviously, in different territories.

DISCUSSION

The duration of molt and its separate stages in an individual. According to the results of studies, includ-

ing those conducted in the 1930s (Miyazaki, 1934; Larionov, 1941; Noskov and Siletskii, 1969; Gwinner et al., 1971), the individual duration of the autumn molt in birds kept under different experimental conditions depends on the photoperiod; with short daylengths, the duration of molt is reduced. The adaptive significance of reducing the duration of molt in birds that begin replacing their plumage in later terms is obvious, since it allows such individuals of migratory species to begin flying away in time, and sedentary species to prepare for wintering. An analysis of the influence of photoperiod on the post-juvenile molt, carried out under the supervision of Prof. G.A. Noskov on 29 species of passerine birds, demonstrated that, in birds inhabiting temperate latitudes, this influence varies within wide limits (Noskov, 1977; Noskov and Smirnov, 1986; Iovchenko and Smirnov, 1987; Noskov et al., 1999, 2018; Filimonova and Starikov, 2006; Noskov and Rymkevich, 2010; Savinich, 2015). The impact is minimal for long-distance migrants and maximal for nomadic species. Thus, in the migratory garden warbler, the duration of molt decreased, on average, by 17 days (30%), and in the nomadic species, the siskin, it decreased by 2–3 times. At the same time, it was shown that subarctic species and populations of widespread species inhabiting the subarctic are much less able to adjust the duration of molt due to the photoperiodic response, since this is prevented by long daylength throughout most of the post-nesting period (Ryzhanovskii, 1997, 2008, 2023). Despite the large amount of evidence of photoperiodic control of molt duration under experimental conditions, there is very little evidence from natural data of a reduction in molt duration at later calendar dates and, accordingly, shorter daylength.

According to our experimental data, molt was significantly shorter in the short-day photoperiod group than in the long-day photoperiod group and the natural daylength group. However, the differences did not exceed ten days (15%). This confirmed that the response to short-day photoperiods shortens the molt duration in bramblings, but, as in many subarctic species (Ryzhanovskii, 1997), within relatively small limits.

Using the interstage interval (the time between recording one stage and the next), we were able to compare the duration of successive molt stages using both experimental and natural data. Using this methodological approach, we were able to demonstrate, based on experimental data, that with decreasing daylength, the duration of molt decreases due to a shortening of the interval, at least between stages 1 and 2 and 2 and 3. Based on repeated observations of bramblings in the wild, a reliable trend was revealed for a decreasing interval between stages 2 and 3 and 3 and 4, depending on the date of the first of the two observations. Thus, analysis of the data obtained in the wild showed that the duration of the initial molt stages

depends on the calendar timing of their occurrence, thereby indirectly confirming the presence of photoperiodic control over the duration of post-juvenile molt in bramblings. In turn, this indicates the existence of directional individual variability in the duration of molt of first-year birds, with a decrease at later dates of onset.

Previously, when studying the sequence of feather replacement during post-juvenile molt in bramblings, it was shown that feathers from different parts of the plumage, including those that determine the onset of these stages, begin to molt during the first four stages (Rymkevich et al., 1990). Therefore, the observed reduction in the duration of interstage intervals indicates a more coordinated entry of the feathers being replaced into molt. Synchronizing the onset of new feather growth is the primary means of regulating the duration of molt for most species (Rymkevich et al., 1990).

Duration and timing of molt seasons. Comparison of post-juvenile molt seasons of bramblings at four points of the range revealed a number of differences between them. The duration of the total season increases in the order Lower Ob region (NE in the studied part of the range)—White Sea region (NW)—Middle Ob region (SE)—Ladoga region (SW). It was 39, 64, 92, and 116 days, respectively. Almost in the same order, the dates of these seasons shift reliably from early to late. The median dates of catching molt birds are August 24 in Lower Ob region, August 28 in White Sea region, September 1 in Ladoga region, and September 10 in Middle Ob region. With an early start of the total molt season in Ladoga region (July 2), its end was the latest (October 25), and the duration is twice as long as the duration of individual molt. In the Lower Ob region, despite the late start of the season (August 1), it ends earlier than in the other study sites (September 8), and its duration is almost half that of individual molt periods. Why is the total season in the Lower Ob region significantly shorter than individual molt periods? Why, given the early nesting periods observed in the Ladoga and Middle Ob regions, are the molt seasons the latest there? Answering these questions is only possible by considering the location of the study sites within the nesting part of the range, the biotopic features of the study sites, the nature of migratory behavior, and the ratio of bird numbers at different molt stages.

Bramblings nest in all the studied areas. In the White Sea and Middle Ob regions, they are quite numerous during nesting in forested taiga biotopes. In the Ladoga region, birds of this species are found nesting in small numbers and, apparently, not every year (Malchevskii and Pukinskii, 1983; Noskov et al., 2020). In the Lower Ob region, bramblings are also relatively few in number during the reproductive period, as they penetrate the forest—tundra and nest at high densities only in forested river valleys (Ryzha-

novskii, 2023). Molt of young birds begins at an early age (22–26 days), when the birds are still in the brood or begin rocking movement (Ryzhanovskii, 1997, 2023)—the first migration in the annual cycle, juvenile migration. Therefore, birds at the beginning of molt are certainly local bramblings.

In the Lower Ob region, young bramblings are almost never captured during post-nesting period, and those that are captured are in the early and, to a lesser extent, middle stages of molt. The sharp decline in the number of young bramblings during post-nesting period in the subarctic and its significant increase in the northern taiga zone indicate that the young of this species, having become independent, migrate from the forest—tundra to the northern taiga (Rogacheva et al., 1983; Ryzhanovskii, 2023). Thus, the post-juvenile molt season in the Lower Ob region is formed by the initial stages of plumage change in bramblings born in the Lower Ob region. This explains the earliest timing of the molt season and its minimal duration, despite the relatively late nesting season for adults.

In the taiga zone of the White Sea region, during post-nesting period bramblings concentrate around small villages surrounded by vegetable gardens, where they find abundant food sources by feeding on weed seeds. Birds from stages 2–4 predominate in captures here. The concentration of such birds and the high number of recaptures indicate that young bramblings migrate to this study area primarily from other territories and reside here during the intensive plumage change. The almost complete absence of birds at stages 5 and 6 indicates that birds at these stages of molt are already joining the autumn migration. Clearly passing bramblings, in stage 7 of molt, account for only a tenth of those molt. The molt season in the White Sea region is dominated by birds that emerged as a result of juvenile migration and settled there for molt. Therefore, it occurs later than in the Lower Ob region.

In the Middle Ob region, bramblings were captured early in the season, either from broods born near the station (not yet molt or at the beginning of molt) or just after the breakup of the brood (at the beginning of molt). Their proportion of all captured birds was extremely small. The number of birds participating in juvenile migration gradually increased from stage 2 to stage 4. The complete lack of recaptures of these bramblings is likely due to the fact that forest habitats in the taiga zone are ill-suited for long-term stopovers during the intense molt, and the birds continue to migrate. During the autumn migration (birds from stages 5–7), the number of molt bramblings is twice as large as during the juvenile migration. This determines the late timing of the molt season in the Middle Ob region. The longer duration of the molt season than in the two previous territories is determined by the presence in the catches of both molt local birds (stage 1) and migratory birds from remote territories (stage 7).

In the Ladoga region, bramblings are encountered with the onset of molt earlier than in other locations. This is consistent with the earlier arrival of spring and the onset of nesting. Since bramblings nest in the Ladoga region in small numbers and not annually, the proportion of young birds captured during the first half of the molt is small. During the autumn migration, on the other hand, when birds that have almost completed their plumage change (stage 7) fly alongside molted birds, bramblings are most numerous, making the post-juvenile molt season in the Ladoga region the latest. The longer duration of the total molt season than in the Middle Ob region is explained by the earlier birth of young in some years.

Thus, the molt season is in most cases formed by birds born in different areas, including local birds in the initial stages of molt, and passaging birds completing their plumage change. The question remains as to whether birds in the middle stages are captured as transients, finishing their juvenile migration, or as permanent residents during the period of intensive plumage change. At all study sites, except the Lower Ob region, there was an increase in the number of molt birds from stage 2 to stage 4. This may be partly due to photoperiodic control of molt rates. An increase in the rate of molt in birds born later leads to greater synchronization of the middle and final stages, compared to the initial ones. For example, individuals that began stage 2 at different times may simultaneously reach stage 4. However, we believe that the main reason for the increase in the number of birds in captures from stage 2 to stage 4 is the influx of birds from different territories with different dates of the onset of molt. This is supported by the much shorter intervals between the medians of most successive stages in the molt season in the White Sea region (Table 3) than the average duration of interstage intervals for these same individual molt stages, determined there from repeat captures (Table 2). The different origins of birds with middle molt stages are also confirmed by the much longer intervals between the medians of stages 2 and 3 in the Ladoga region, and stages 3 and 4 in the Middle Ob region (Tables 2, 3), than the interstage intervals of individual molt.

Our data on the directional intraseasonal variability of the individual duration of molt and the heterogeneous population structure of birds, which can vary dramatically during the molt season at different points in the range, also have practical significance. In particular, the method of Underhill and Zucchini (1988), which is becoming increasingly popular among molt researchers, was developed to determine individual molt duration, the average date of its onset, and the variability of this date in the population based on a set of single captures of molt birds. This method and its extended model (Boersch-Supan et al., 2024) are based on the assumptions that all individuals have the same duration of molt and that the onset dates of molt

are normally distributed. Neither assumption is true for post-juvenile molt. The duration of molt is reduced in birds that molt later, and the distribution of onset dates of molt following the distribution of hatching dates will not be normal, at least for species that, like the brambling, begin their plumage change at a uniform age. Most importantly, the composition of the molt group of birds will influence the results. The models proposed assume a homogeneous population structure for the species in the study area. As our research has shown, birds hatched in different areas, with different molt dates and, occurring in different numbers, may molt in the same area. Therefore, for migratory species, including those with a nomadic form of migration behavior, which includes the brambling, the average date of onset of post-juvenile molt obtained in one location is generally not a population characteristic.

CONCLUSIONS

The response to short-day photoperiods shortens the duration of post-juvenile molt in bramblings, but to a relatively small extent. With shorter daylength, the duration of molt decreases due to a shortening of the initial stages of molt, as evidenced by data from a photoperiod experiment. Data from repeated captures of molt bramblings in the wild revealed a reduction in the duration of the initial stages of molt at later plumage replacement dates, thereby indirectly confirming the presence of directional adaptive variability in the individual duration of molt in bramblings under the influence of the photoperiod response.

The post-juvenile molt season in the Lower Ob region is dominated by individuals born in the Lower Ob region and are in the early stages of plumage change. During the molt season, the study area of the White Sea region is primarily inhabited by birds that removed there during juvenile migration to undergo the mid-molt stages. The Ladoga and Middle Ob regions contain both local birds that have just begun molt and birds from remote areas that reside here during the mid-molt stages or are completing their plumage change during autumn migration. The presence of both local and transit birds in the Ladoga and Middle Ob regions makes the molt seasons the longest, and the predominance of individuals completing their plumage change makes the molt seasons the latest.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The methods of capturing and keeping birds and the protocols of photoperiodic experiments were approved by the Bioethics Commission of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Protocol no. 17 of January 24, 2025).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

- Boersch-Supan, P.H., Hanmer, H.J., and Robinson, R.A., Extended molt phenology models improve inferences about molt duration and timing, *Ornithology*, 2024, vol. 141.
- Burskii, O.V., Logistic model of body costs during postbreeding molt in birds, *Zool. Zh.*, 2015, vol. 94, no. 3, pp. 544–599.
- Filimonova, N.S. and Starikov, D.A., Photoperiodic control of the formation of additional areas of juvenile plumage and postjuvenile molt in the tree pipit *Anthus trivialis* (L.), *Ornitologicheskie issledovaniya v Severnoi Evrazii. Tez. XII Mezhdunarodnoi ornitol. konf. Severnoi Evrazii 31 yanvarya–5 fevralya 2006, Stavropol'* (Ornithological Studies in Northern Eurasia, XII Int. Ornithol. Conf. of Northern Eurasia, January 31–February 5, Stavropol, Abstracts of Papers), Stavropol, 2006, pp. 533–534.
- Gwinner, E., Berthold, P., and Klein, H., Untersuchungen zur Jahresperiodik von Laubsängern. II. Einfluß der Tageslichtdauer auf die Entwicklung des Gefieders, des Gewichts und der Zugunruhe bei *Phylloscopus trochilus* und *Ph. collybita*, *J. Ornithol.*, 1971, vol. 112, pp. 253–265.
- Iovchenko, N.P. and Smirnov, E.N., Postjuvenile molt of the siskin and features of its photoperiodic regulation, *Issledovaniya po faune i ekologii ptits Palearktiki* (Studies on the Fauna and Ecology of Palearctic Birds), Leningrad, 1987, pp. 16–33. (Tr. Zool. Inst. Akad. Nauk SSSR, vol. 163).
- Jenni, L. and Winkler, R., *Moult and Ageing of European Passerines*, Academic, 1994.
- Larionov, V.F., Reduction of the molting period of birds by abruptly changing the length of the day, *Dokl. Akad. Nauk SSSR*, 1941, vol. 33, no. 3, pp. 227–229.
- Mal'chevskii, A.S. and Pukinskii, Yu.B., *Ptitsy Leningradskoi oblasti i sopredel'nykh territorii* (Birds of the Leningrad Oblast and Adjacent Areas), Leningrad: Leningr. Univ., 1983, vol. 2.
- Miyazaki, H., On the relation of the daily period to the sexual maturity and to the moulting of *Zosterops palpebrosa japonica*, *Sci. Rep. Tohoku Imp. Univ. Biol. Ser.*, 1934, no. 9, pp. 183–203.
- Newton, I., Molt and plumage, *Ringing Migr.*, 2009, vol. 24, no. 3, pp. 220–226. <https://doi.org/10.1080/03078698.2009.9674395>
- Noskov, G.A., Molt of the chaffinch (*Fringilla coelebs*). Photoperiodic regulation and place in the annual cycle, *Zool. Zh.*, 1977, vol. 56, no. 11, pp. 1676–1686.
- Noskov, G.A., Terminology used, *Migratsii ptits Severo-Zapada Rossii. Nevorob'inye* (Bird Migrations of North-West Russia. Non-Passeriformes), St. Petersburg, 2016, pp. 16–19.
- Noskov, G.A. and Gaginskaya, A.R., On the methodology of describing the state of molt in birds, *Soobshch. Pribalt. Kom. Izuch. Migr. Ptits* (Tartu), 1972, no. 7, pp. 154–163.
- Noskov, G.A. and Rymkevich, T.A., Regulation of the parameters of the annual cycle and its role in the microevolutionary process in birds, *Usp. Sovrem. Biol.*, 2010, vol. 130, no. 4, pp. 346–359.
- Noskov, G.A. and Siletskii, V.V., On photoperiodic regulation of the timing of juvenile molt in some passerine birds, *Ornitologiya v SSSR* (Ornithology in the USSR), Ashkhabad, 1969, no. part 2, pp. 456–459.
- Noskov, G.A. and Smirnov, E.N., Some features of photoperiodic control and completeness of postjuvenile molt in the common redpoll, *Aktual'nye problemy ornitologii* (Actual Problems of Ornithology), Moscow, 1986, pp. 69–75.
- Noskov, G.A., Rymkevich, T.A., and Iovchenko, N.P., Intraspecific variation of moult: adaptive significance and way of its realization, *Proceedings of the 22nd International Ornithological Congress, August 1999, Durban, South Africa*, Johannesburg, 1999, pp. 544–563.
- Noskov, G.A., Rymkevich, T.A., and Smirnov, E.N., Postjuvenile molt in the common crossbill (*Loxia curvirostra curvirostra*): photoperiodic regulation and its role in synchronization of the annual cycle, *Biol. Bull.* (Moscow), 2018, vol. 45, no. 7, pp. 718–731.
- Noskov, G.A., Gaginskaya, A.R., Panov, I.N., and Rymkevich, T.A., Brambling (*Fringilla montifringilla*), *Migratsii ptits Severo-Zapada Rossii. Vorob'inye* (Migrations of Bird of North-West Russia. Passeriformes), St. Petersburg: ANO LA Professional, 2020, pp. 376–381.
- Panov, I.N., Overlap between moult and autumn migration in passerines in northern taiga zone of Eastern Fennoscandia, *Avian Ecol. Behav.*, 2011, vol. 19, pp. 33–64.
- Rogacheva, E.V., Ravkin, E.S., Syroechkovskii, E.E., and Kuznetsov, E.A., Fauna and bird population of the Yenisei forest-tundra, *Zhivotnyi mir eniseiskoi lesotundry i prirodnaya zonal'nost* (Animal World of the Yenisei Forest-Tundra and Natural Zonality), Moscow: Nauka, 1983, pp. 14–47.
- Rymkevich, T.A., Mogil'ner, A.I., Noskov, G.A., and Yakovleva, G.A., New indices for characterizing molt in passerine birds, *Zool. Zh.*, 1987, vol. 66, no. 3, pp. 444–453.

- Rymkevich, T.A., Savinich, I.B., and Noskov, G.A., *Lin'ka vorob'inykh ptits Severo-Zapada SSSR* (Molt of Passerine Birds in the North-West of the USSR), Leningrad: Leningr. Gos. Univ., 1990, pp. 287–292.
- Ryzhanovskii, V.N., *Ekologiya poslegnezhdovogo perioda zhizni vorob'inykh ptits Subarktiki* (Ecology of the Post-Breeding Period of Life of Passerine Birds of the Subarctic), Yekaterinburg: Ural. Univ., 1997.
- Ryzhanovskii, V.N., The role of photoperiodic conditions in the life of high-latitude passerine birds, *Zool. Zh.*, 2008, vol. 87, no. 6, pp. 732–747.
- Ryzhanovsky, V.N., Ecology of the brambling *Fringilla montifringilla* L. in the northern part of Western Siberia, *Biol. Bull.* (Moscow), 2023, vol. 6, pp. 1401–1410. <https://doi.org/10.1134/S1062359023602847>
- Savinich, I.B., Formation of plumage in the European robin *Erithacus rubecula* in the first year of life and photoperiodic regulation of postjuvenile molt, *Russ. Ornitol. Zh.*, 2015, vol. 24, no. 1195, pp. 3489–3494.
- Strel'nikov, E.G., Molt of passerines as a tool for ornithological monitoring, *Vestn. Tver. Gos. Univ., Ser. Biol. Ekol.*, 2019, no. 1 (53), pp. 218–232.
- Stresemann, E. and Stresemann, V., Die Mauser der Vögel, *J. Ornithol.*, 1966.
- Underhill, L.G. and Zucchini, W., A model for avian primary moult, *Ibis*, 1988, vol. 130, no. 3, pp. 358–372.
- Voitkevich, A.A., *Pero ptitsy* (Bird's Feather), Moscow: Akad. Nauk SSSR, 1962.

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