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Subspecies-specific Features of Molt in the Common Chiffchaff (*Phylloscopus collybita* L.) from Europe and Western Siberia

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Abstract—The patterns of molt in the chiffchaffs of the nominotypical subspecies from central Europe and eastern European subspecies from the Ladoga region are compared with that of the Siberian subspecies from the lower Ob region. The onset dates of postjuvenile molt in the Siberian subspecies are controlled endogenously, while in the nominative and, probably, eastern European subspecies they are under photoperiodic control. The molt of chiffchaffs from central Europe is no less complete than in birds from the Ladoga region and more complete than in Siberian birds. The individual duration of molt is the shortest in Siberian birds and the longest in central European birds, being intermediate in birds from the Ladoga region. Differences in the pattern of postnuptial molt between chiffchaffs from the Ladoga and Ob regions concern its duration and completeness. The completeness of molt proved to be reduced in half of examined birds from the Ladoga region and in some birds from the Ob region. The duration of complete molt in birds from the Ob region is smaller (40 days vs. 60 days in birds from the Ladoga region) at a longer daylight period, which is evidence for a higher rate of feather growth. The completeness and timing of prenuptial molt do not differ between the subspecies.

Keywords: common chiffchaff, molt, timing, completeness, photoperiodic control, endogenous control

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According to *The Species List of Birds of the Russian Federation* [1], chiffchaffs nesting in Russia belong to three subspecies: eastern European *Phylloscopus collybita abietinus*, Siberian *Ph. c. tristis,* and Caucasian *Ph. c. caucasicus*. Western Europe is populated by the nominotypical subspecies *Ph. c. collybita* [2, 3] The eastern distribution boundary of this subspecies is not clearly demarcated, but it is known to nest in Germany. The eastern European subspecies populates Scandinavia and part of East Europe; Siberian birds live not only all over Siberia but also expand to Europe. The boundary between the eastern European and Siberian subspecies passes west of the Urals, approximately from the Kanin Peninsula to Orenburg [4]. Eastern European chiffchaffs occur and probably nest in Sverdlovsk oblast [5], but only Siberian chiffchaffs have been recorded and trapped in in the polar Urals, lower Ob region, and Yamal. It is noteworthy that eastern European and Siberian birds as subspecies are not represented solely in ornithological collections of taxonomists, as it occurs sometimes, but can be readily distinguished by the song in the field. There is a zone of hybridization [4] where birds with a "hybrid" song occur. Korovin [5] described such a song of a male chiffchaff in Nevyansky district of Sverdlovsk oblast (a single recording in the region where Siberian chiffchaffs are common). The bird sang the "European monosyllabic" and "Siberian disyllabic" variants of the song and, in addition a combined song in which the Siberian variant prevailed slightly.

The ornithological literature provides data on the molt of chiffchaffs of the nominotypical [6, 7] and eastern European subspecies [8] and on certain differences in the process of plumage regeneration between them, while we have data on the molt of Siberian chiffchaffs, which also differs from that of other subspecies. The purpose of this study was to analyze variation in the pattern of molt over the species range in order to reveal factors responsible for the differences between the subspecies.

MATERIAL AND METHODS

The chiffchaff is not abundant but ubiquitous in the Ob forest–tundra. The birds were caught with mist nets and traps in the vicinity of Labytnangi (66°40′ N, 66°40′ E). Only single birds were trapped in spring and early summer, but their number increased in August and early September to 1–3 ind. per day in some years or per week in other years. On the whole, descriptions of plumage were made for 129 young and 41 adult chiffchaffs. The birds were trapped mainly between 1977 and 1982, but single individuals were also collected in the subsequent period (until 2013). In addition, seven chicks of the same brood aged 11–12 days were taken from the nests and reared in captivity until the end of molting, being fed ant eggs and mealworms. Thee chicks were kept under a short-day photoperiod (16L : 8D in mid-July, with daylight length decreasing by 30 min every 5 days to 12L : 12D в начале сентября); the other four lived under a photoperiod natural for the Arctic Circle latitude (from 24L : 0D in mid-July to 16L : 8D in early September. Two adult females collected together with the chicks were kept at a natural photoperiod until the end of molting, and two adult males trapped in mid-August were kept in an aviary for 20 days.

To study the prenuptial molt, two adult males and two young birds were trapped in late July, delivered to the Middle Urals, and kept there until the next summer under the following photoperiodic conditions: 17L : 8D in early August to 12L : 12D in late September, 11L : 13D from early October to late November, and 14L : 10D from early December to late March, with subsequent natural increase in daylight length outdoors. In September 2015, 27 young of the year of the Siberian subspecies were trapped in the Middle Urals and four of them were kept in cages until the next summer. Between early October and February 15, the daylight length was reduced to 11 h (11L : 13T) to make it similar to that in the wintering grounds of the species in northern India and Pakistan [2]. Thereafter, the photoperiod was changed to 12L : 12T and remained so until the natural increase in daylight length. The plumage was examined every 5 days during molt and every 10 days in the absence of molt and described according to the procedure by Noskov and Rymkevich [9]. Records of bird weight and body condition were also taken during each examination. The average duration of molt was calculated by regression analysis based on capture dates of molting birds [10]. To monitor the process of molt, the plumage was stained with an alcohol solution of rhodamine.

RESULTS

The annual cycle of the chiffchaff includes two molts: postjuvenile (in young birds) and postnuptial (in adult birds in the nesting range) or prenuptial (in immature and adult birds on wintering grounds).

Molt in nominotypical subspecies. The postjuvenile molt is incomplete but extensive (Table 1) and involves the replacement of head and body coverts, 5–6 inner upper major secondary coverts, all median and minor secondary coverts, and, in many birds, tertiary flights and central rectrices [6]. Birds reared under natural photoperiod started molting at the age of 58–76 (68 ± 5.8) days [6], compared to 32–35 days under a 12L : 12D photoperiod [7]; i.e., the timing of molt was definitely under photoperiodic control. The onset of molt in the former group was observed 2–4 weeks after the second phase of juvenile feather growth was completed [10]. The age of birds at this stage was 25–40 days. The duration of postjuvenile molt in these birds was 61 ± 8.9 days at a natural photoperiod [6], 40 days at a constant short-day photoperiod (12L : 12T), and 80 days at a constant long-day photoperiod (18L : 6T) [7].

The postnuptial molt in adult birds is complete, starts in late June to August, and lasts for 60–70 days [6]. The prenuptial molt takes place in December to January and is incomplete: head and body coverts and, in some birds, tertiary flights and central rectrices are replaced. Wing coverts are not involved in this process [3].

Molt in eastern European subspecies (from Ladoga region). The postjuvenile molt involves the replacement of head and tail coverts and part of wing coverts, including all upper secondary coverts, upper coverts of the propatagium, alular coverts, upper and under carpometacarpal coverts, under major primary coverts, under median secondary coverts, and under coverts of the propatagium. In addition, tertiary flights and central rectrices are replaced in some birds (Table1). The second phase of juvenile feather growth starts at the age of 25–30 days and is completed by day 40–45, which coincides with the onset of molt. The timing of molt is apparently under photoperiodic control, because birds from the first breeding cycle (May–June) started molting on days 39–40 after hatching ($n = 3$), while birds from the second cycle (July), on days 32–34 ($n = 3$). The duration of molt in the former group was 46–58 (51 ± 0.9) days; in the latter group (indirect data), 36–46 days. Migration to wintering quarters begins at the final stages of postjuvenile molt or after its completion [8].

According to the same author [8], the postnuptial molt was complete in half of examined birds; in the others, inner secondary flights and part of upper and under wing coverts were not replaced. The molt did not coincide with nesting and continued for about 60 days.

The prenuptial molt (in December to January) is incomplete and involves the replacement of head and body coverts, tertiary flights, tertiary coverts, and central rectrices (in some cases, all of them) [3].

Molt in Siberian subspecies. The postjuvenile molt is still less complete than in the first two subspecies. Body coverts in birds caught with mist nets and traps were replaced to the degree common to passerine birds (feathers grown in the nest). Wing molt involved the replacement of upper median secondary coverts (mostly inner) in the majority of birds and, in some birds, of inner upper major secondary coverts and upper minor secondary coverts. The upper and under coverts of the propatagium, upper and under carpometacarpal coverts, under median secondary coverts, and under tertiary coverts were also replaced in some birds (Table 1).

The completeness of molt did not differ appreciably within the group of four captive chiffchaffs reared under a natural photoperiod but was significantly lower in the group of three birds reared at a relatively short-day photoperiod with decreasing daylight length (16L : 8T). No replacement of upper and under wing coverts was observed in any of the birds. Part of upper

Table 1. Completeness of (I) postjuvenile, (II) postnuptial, and (III) prenuptial molts in the main common chiffchaff subspecies of northern Eurasia: (•) molt in all birds, (◊) molt in part of birds, (?) no data, (–) no molt

Feather tracts and their regions	*Ph. c. collybita*			*Ph. c. abietinus*			*Ph. c. tristis*		
	I [6]	II [6]	III [3]	I [8]	II [8]	III [3]	I	II	III
Capital	•	•	•	•	•	•	•	•	•
Ventral	•	•	•	•	•	•	•	•	•
Spinal	•	•	•	•	•	•	•	•	•
Humeral	•	•	•	•	•	•	•	•	•
Femoral	•	•	•	•	•	•	•	•	•
Crural	•	•	•	•	•	•	•	•	•
Anal	•	•	•	•	•	•	•	•	•
Rectrices	◊	•	◊	◊	•	◊		•	◊
UpTC	•	•	•	•	•	•	•	•	•
UnTC	•	•	•	•	•	•	•	•	•
PF		•			•			•	
SF		◊			◊			◊	
TF	◊	•	◊	◊	•	◊		•	◊
UpMjPC		•			•			•	
UpMdPC		•			•			•	
UpMjSC	•	•		•	•		◊	•	
UpMdSC	•	•		•	•		◊	•	
UpMnSC	•	•		•	•		◊	◊	
UCP	•	•		•	•		◊	•	
CC	•	•		•	•			•	
AR		•			•			•	
AC	•	•		•	•			•	
UpCC	•	•		•	•		◊	•	
UnCC	•	•		•	•		◊	•	
UnMjPC	?	?			◊			◊	
UnMdPC	?	?			◊			◊	
UnMjSC	?	?			◊			◊	
UnMdSC	•	•		•	•		◊	•	
UnTC	•	•		•	•		◊	•	
Apteria	•	•		•	•		•	•	

Regions of feather tracts: PF, primary flights; SF, secondary flights; TF, tertiary flights; UpTC, upper tail coverts; UnTC, under tail coverts; UpMjPC, upper major primary coverts; UpMdPC, upper median primary coverts; UpMjSC, upper major secondary coverts; UpMdSC, upper median secondary coverts; UpMnSC, upper minor secondary coverts; UCP upper coverts of the propatagium; CC, carpal covert; AR, alular remiges; AC, alular coverts; UpCC, upper carpometacarpal coverts; UnCC, under carpometacarpal coverts; UnMjPC, under major primary coverts; UnMdPC, under median primary coverts; UnMjSC, under major secondary coverts; UnMdSC, under median secondary coverts; UnTC, under tertiary coverts.

carpometacarpal coverts were replaced in only two birds, and part of under carpometacarpal coverts, in one bird. All the birds showed partial replacement of upper and under coverts of the propatagium. On the body, no molt of upper and under tail coverts and feathers of the anal tract was observed, only crural feathers were replaced in one bird. The completeness of molt in other body feather tracts was also lower than under natural photoperiodic conditions of the nesting region.

The second phase of juvenile feather growth begins at an age of 15–17 days and continues until day 30–35. Three tagged chiffchaffs from the same brood caught at an age of 23 days had such feathers all over the body. The tree birds reared at a short-day photoperiod started molting at an age of 24–29 days (on average,

Table 2. Capture dates of molting young chiffchaffs by 5-day periods (I –VI)

Stage of molt	July			August						September		
	IV	V	VI	I	II	III	IV	V	VI	I	II	III
No molt					3							
1	1			2	3	4						
2					2	3			1			
3					1	3	6	2	2			
4						1	5	11	2			
5							1	6	6	4	7	
6									10	9	6	2
New plumage									7	9	7	5
Number of birds examined	1	0	0	2	9	11	12	19	28	20	22	5

25.7 days); the four birds reared at a natural photoperiod, at an age of 24–25 (24.2 ± 0.2) days. This is conclusive evidence for endogenous control of the timing of molt in Siberian chiffchaffs. The duration of molt in the respective group was 23–35 (27.0) and 36–40 (38.0 ± 0.9) days.

The process of molt was divided into six stages. Birds that started molting (stage 1) were being trapped between August 2 and 12, but in the phenologicaly early year 1977 one bird was trapped on July 19. Three not yet molting fledglings were trapped on August 8. Since the chicks hatched in the first 10-day period of July, their calculated age at the onset of molt was less than 30 days. Most of young northern chiffchaffs molt in August (Table 2). Birds trapped after August 27 had finished molting. According to regression ($y = 0.144x - 5922.4$), the long-term dates of the onset and end of molt are June 31 and September 11, with the duration of molt averaging 42 days. The latest capture date of a bird completing the molt is September 18,1978 (a phenologically late year). However, the bulk of such birds and individuals in a new plumage were being trapped in the first 10-day period of September, with their proportion among chiffchaffs trapped over the second half of summer reached 42.6%, being higher than in the willow warbler *Ph. trochilus* [12]. This fact indicates that young chiffchaffs become involved in migration at the last stage of molt or after its completion. Premigratory fattening in captive birds began after the end of molt rather than at its last stage, as is usual in the willow warbler. Therefore, their departure from the forest–tundra begins and ends on later dates. Among Sylvidae species, chiffchaffs are the last to leave the Ob forest–tundra. All chiffchaffs trapped in the Middle Urals in the second and third 10-day periods of September had no traces of molt, contained medium amounts of fat, and lagged behind other migrating birds.

The postnuptial molt in northern chiffchaffs may be either complete or incomplete. In the latter case, part or all secondary flights and part of wing coverts are not replaced. Such a pattern was observed in a female trapped with a brood: not only secondary flights, but also upper minor coverts and part of under coverts were not replaced in this bird. In contract, the male from this pair molted completely, as did all six males trapped at the last stage of this process. Apparently, the proportion of birds with an incomplete molt is insignificant. The molt does not coincide with breeding in birds that nest on normal dates: all four birds captured at two nests with 10- to 12-day-old chicks were in the old plumage. One male was accidentally released, and he remaining male and two females started molting on days 19, 27, and 29 after the hatching of chicks, respectively.

Chiffchaffs at the onset of postnuptial molt were being trapped between July 20 and August 7, with birds in the old plumage occurring in catches until July 31 (Table 3). The average onset date of molt according to the regression equation ($y = 0.2462x - 10120$) was July 24. Males prevailed among birds that were the first to start molting, and females prevailed among birds in which this process was delayed. The onset period of molting continued 35–30 days. Two chiffchaffs completing the molt (stage 11) were trapped on August 19 and 20. The average date of the end of molt was September 7; the average duration of molt was 45 days, and that of the molting season, 50–60 days. The male kept in an aviary together with the brood started molting on August 4 and completed this process within 39 days, on September 11. The birds partially lose the ability to fly during the replacement of primary flights and rectrices (stages 7–9) and become involved in the migration process at the latest stages of molt (10–11). Chiffchaffs in the new plumage has sufficient fat reserves and were obviously involved in this process.

The prenuptial molt in captive chiffchaffs born or nesting in the lower Ob region started in the last 5-day period of December, 3 weeks after change in photoperiod from 11L : 13D to 14L : 10D, and was completed in early February. Birds trapped during the autumn migration in the Middle Urals started molting in early

Table 3. Capture dates of molting adult chiffchaffs by 5-day periods (I –VI)

Stage of molt	July				August						September	
	III	IV	V	VI	I	II	III	IV	V	VI	I	II
No molt	2	2	1	1								
1			1	2	3							
2			1		1	1						
3			3	3	1	1		1				
4							1	1				
5					1	1		1				
6							1					
7												
8												
9					1				1			
10									1			
11							1		2			
New plumage											2	3
Number of birds examined	2	2	6	6	7	3	3	3	4	0	2	3

March, 2 weeks after the daylight length was increased from 11 to 12 h.

Th completeness of molt in chiffchaffs from the Ob region and trapped in the Urals did not differ significantly from that in birds from eastern and central Europe. Contour feathers on the head and body were replaced in all captive birds. Feathers replaced in two northern young of the year included the 17th, 18th, and 19th flights and central rectrices; in two birds trapped in the Urals, the 18th flights and central rectrices. Only head and tail feathers were replaced in other birds. The molt continued for 30–35 days, until the end of March.

DISUSSION

In birds with a migratory type of activity, such as the chiffchaff, the molt may differ between geographic populations in timing, rate, and completeness [9]. In birds with a large range, this may serve as a criterion for distinguishing populations [13, 14] and subspecies [15].

In Germany, the molt of chiffchaffs (*Ph. c. collybita*) under experimental conditions started 28 ± 2.0 days after the second phase of juvenile feather growth was completed [6]. In the Ladoga region *(Ph. c. abietinus*), this phase partly overlapped with molt: in birds from an early brood, it continued between days 25–30 and 40–45 after hatching, while the molt started on days 39–40; in birds from the second broods, the molt started on days 32–34 and overlapped with the phase of secondary feather growth by more than 50%. In the lower Ob region (*Ph. c. tristis*), this phase continued between days 15–18 and 40–45, with the molt starting on days 24–25. This overlap is similar to that in Ladoga fledglings from the second broods, but the second phase in the Ob region starts before the transition of fledglings to independent feeding. It appears that the time program of growth and development in Siberian chiffchaffs is different from that in European chiffchaffs of both subspecies. The overlap of the second growth phase and molt results in greater energy expenditures because of increase in the number of growing feathers, but the end of molt and departure shift to earlier dates, which is important under conditions of the Subarctic.

Differences in age at the onset of postjuvenile molt between the subspecies are considerable, especially between birds from central Europe and lower Ob region: the former start molting at the age when this process in the latter is completed, with the main period of molt (August–early September) being the same at both latitudes. The onset of molt in birds from the Ob region is obviously controlled endogenously, since the birds kept at a reduced daylight length (16L : 8T) started molting at the same age as the birds kept under natural photoperiod (21L : 3T). The molt of Ladoga birds is probably under photoperiodic control, because in birds from the first broods it started a week earlier than in birds from the second broods [8]. According to our calculations, this occurred at a daylight length of 18–19 h in the former and 15–16 h in the latter. The difference appears to account for the shift in the timing of molt, but the available data are as yet insufficient for statistical verification.

The dates of molt in chiffchaffs from central Europe are also under photoperiodic control, because at a short-day photoperiod (12L) they started molting a month earlier than at a natural midsummer photoperiod (16L). The minimum age at the onset of molt in both European subspecies in the same (32–35 days), while the maximum age is different: 39–40 days in the

Ladoga region vs. 58–76 days in Germany, despite that the natural daylight length in the Ladoga region is greater. Therefore, the European subspecies differently react to this factor. Eastern European chiffchaffs at the northern limit of the range (70° N), at a photoperiod of 24L : 0D until the end of July (taking into account refraction), start molting in the first half of August, at an age of no more than 40 days. The molt of western European chiffchaffs under the same conditions would start only at the age of 60–70 days, at the end of August, which is too late. Hence, chiffchaffs nesting in Scandinavia are represented by the east European subspecies *Ph. c. abietinus* adapted to the light regime of Arctic latitudes.

Differences in the completeness of molt in birds from the Ob region, compared to birds from the Ladoga region and central Europe, are observed in the wing feather tracts. Birds with the completeness of molt characteristic of the Ladoga region and Germany (with the replacement of all upper secondary coverts) and with the replacement of tertiary coverts and central rectrices have not been trapped in the Subarctic (Table 1). Taking into account photoperiodic conditions of these regions (with the daylight length in the Subarctic being greater and decreasing at a lower rate), the situation should have been inverse, since the completeness of molt in experiments with birds from the same region (Siberia) was lower in the group kept at a short-day photoperiod. Thus, the dependence of this parameter on photoperiod is not observed at the level of species range, unlike within subspecies ranges where a certain photoperiodic interval is characteristic of each subspecies [16]. Within this interval, the completeness of molt decreases with reduction in daylight length.

The individual duration of postjuvenile molt is minimum in birds from the Ob region, maximum in central European birds, being intermediate in birds from the Ladoga region. The greater duration of molt in Ladoga birds, compared to Ob birds, is justified, because its completeness is higher. Since the molt in chiffchaffs of the nominotypical subspecies continues for more than 2 months, its completeness should be higher than in the east European subspecies (this has not been confirmed but is possible).

The pattern of postnuptial molt in chiffchaffs of the nominotypical and eastern European subspecies is similar, but Siberian birds differ from European in the duration and completeness of molt. As a rule, the more feathers are replaced, the longer is the molt. The postnuptial molt of the chiffchaff in the maximum variant is complete. A decrease in its completeness occurs in both Ladoga and Ob regions but has been observed in about half of birds examined in the former region [8] and in only a few birds from the latter region. As shown by Noskov and Rymkevich [16], this decrease takes place beyond the limits of photoperiodic intervals appropriate for molt. In late-molting birds (e.g., rearing the second brood), the final stages of molt coincided with a decrease in daylight length below the lower threshold of the photoperiodic interval, and the replacement of inner flight feathers stopped. The second nesting cycle is common for chiffchaffs in the Ladoga region, and the proportion of birds with a partial molt is relatively large there. In the Ob region, chiffchaffs complete only one nesting cycle, and few of them start molting with a delay; hence, the proportion of birds with a partial molt is small. In addition, the daylight length in the north decreases at a lower rate. At the end of August, the daylight length at 60° N is about 14 h, while that at the Arctic Circle (65°60' N) is 15 h. It may be that the latter regime allows a complete molt, while the former does not; i.e., the photoperiodic intervals in chiffchaffs from the Ladoga and Ob regions are similar. The smaller duration of complete molt in birds from the Ob region (40 days, compared to 60 days in the Ladoga region) at a greater daylight length is evidence for a higher rate feather growth in the Siberian subspecies.

The completeness and timing of the prenuptial molt are equal in all three chiffchaff subspecies. Apparently, their way of life does not make necessary the renewal of flights and rectrices twice a year, unlike in birds migrating to Africa (the willow warbler) and Southeast Asia (Arctic warbler *Ph. borealis*) in which the prenuptial molt is complete.

Thus, subspecies-specific features of the annual molt cycle in the common chiffchaff are manifested primarily in different reactions to photoperiodic conditions in the nesting range of a given subspecies. The length of migration route may also have an effect: it is greater for the Siberian subspecies, making it necessary to start migrating earlier than the European subspecies. Accordingly, the northern birds are characterized by the earlier onset, shorter duration, and lower completeness of postjuvenile molt.

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