

Wing moult in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis*

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Most long-distance passerine migrants in Sweden moult on breeding grounds before leaving on autumn migration to winter quarters. However, birds laying second or replacement clutches, or just breeding late, have too little time for a normal moult on the breeding grounds. When time is limited the birds may respond by making various adjustments to the moult, for example by moulting more quickly or by suspending the moult. In this study, the relationship between the performance of post-nuptial remex moult in Common Whitethroats breeding on Gotland, southeast Sweden, and autumn migration departure was investigated. The majority (77%) of the birds had interrupted moult in either the primaries or secondaries. Interruption of moult was more common among birds with a later onset date, as was asymmetry in moult between wings. The interruption of moult led to a significant time gain and moult completion was, consequently, more synchronized than moult onset. The results from this study indicate, in accordance with other data, that an early start of autumn migration is important. An early start may be crucial to facilitate the crossing of the Sahara Desert once the dry season has begun.

Birds must moult regularly to maintain a functional plumage. Moult is costly, both in terms of energy requirements (for a review see Lindström *et al.* 1993) and in increased predation risk (Slagsvold & Dale 1996) due to impaired flight performance (Haukioja 1971, Tucker 1991, Swaddle & Witter 1997), and the timing of moult is therefore crucial. As with other events in a bird's life, the timing of moult is governed by a circannual rhythm that is finely tuned by environmental cues, such as photoperiod (e.g. Gwinner 1996). Most Palearctic passerines moult annually after breeding and before autumn migration, but moult in the winter quarters is also common in long distance migrants (see Svensson 1992).

If breeding performance is extended, the time available for moult may not always be enough for a normal complete moult. In this case moult may start before breeding is over. The resulting moult/breeding overlap can have severe costs in terms of reproductive fitness. Hemborg and Lundberg (1998), in an experiment with Pied Flycatchers *Ficedula hypoleuca*, showed that body condition during breeding, and survival to the next

year of both parents and nestlings, were lower among birds with experimentally induced moult/breeding overlap than among control birds. Similarly, in the Blue Tit *Parus caeruleus*, Nilsson and Svensson (1996) showed fitness costs in reduced insulation capacity of the plumage, as well as costs in increased nestling mortality (Svensson & Nilsson 1997) as a result of induced moult/breeding overlap. In spite of the costs, a slight moult/breeding overlap frequently occurs in several species (review in Jenni & Winkler 1994, Hemborg *et al.* 1998). In contrast, an overlap between moult and migration is rarely found, and then only at very low intensity (Jenni & Winkler 1994). Since moult impairs flight performance (Haukioja 1971, Tucker 1991, Swaddle & Witter 1997), an overlap between moult and migration may be costly. When time is short it might be better to shorten the moult period, either by suspending parts of the moult until the bird reaches the winter quarters, or by adjusting the moult performance. In an experiment with Lesser Whitethroats *Sylvia curruca* we (Hall & Fransson, ²⁰⁰⁰ ~~in press~~) showed that birds moulting under time-constraint, induced by shortened photoperiod, moulted faster and grew shorter remiges than birds without a time-constraint.

In this study, the post-nuptial remex moult of

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Common Whitethroats *Sylvia communis* (hereon: Whitethroat) on the breeding grounds on Gotland, southeast Sweden, was analysed to study the relationship between the performance of post-nuptial moult and the timing of departure on autumn migration. This is one of few studies in which this relationship has been investigated. The Whitethroats on Gotland are of the nominate subspecies *S. c. communis*, which normally moults in the breeding quarters, after breeding but before autumn migration. This contrasts with the eastern subspecies *S. c. icterops*, which usually moults in the winter quarters. Suspended moult occurs in both subspecies, although not as the main strategy (Svensson 1992). Understanding the moult performance of the Whitethroat is complicated by the occurrence of intermediate birds, and a rather extensive pre-nuptial moult in the winter quarters in birds of the nominate subspecies. This sometimes includes both secondaries and primaries (Jenni & Winkler 1994).

MATERIAL AND METHODS

Whitethroats were trapped in mist-nets from 29 July to 9 September during 1989–94 at different localities at the southernmost part of the island of Gotland (56°55'N 18°8'E). All birds were ringed, aged following Svensson (1992), weighed, examined for subcutaneous fat loads (Pettersson & Hasselquist 1985) and had wing length (maximum chord, Svensson 1992) measured before immediate release at the trapping sites. Adult birds were examined for post-nuptial remex moult or traces of moult and this was recorded on moult cards. Moult was normally recorded on both wings. When individuals were trapped several times, a moult card was filed for each trapping occasion.

In total, 109 moult cards were collected from 89 individual Whitethroats. So that only one moult card from each individual should be used in each analysis, when birds were trapped in more than one year, only the first year was used. Moult was scored in tenths of full feather length following Sondell (1977). This method gives a total moult score of 15 for each wing (nine primaries plus six secondaries) when moult is completed. Primaries were numbered descendantly, from primary 1 at the carpal joint outwards to primary 9 at the wing tip. The minute primary 10 was not considered in this study. Secondaries were numbered ascendantly from the carpal joint inwards towards the body.

Once all the remiges have been shed, it is possible to judge whether the moult of a bird will be completed.

However, if the moult is to be interrupted, it is possible to judge when the most recent growing feather has passed a point where the next unmoulted feather should have been shed. During active moult, Whitethroats in this study shed the remiges at an interval of 0–0.4 moult scores. Based on this, we consider moult to have been interrupted if the shortest growing feather reached half of its full length without any of the remaining old feathers being shed. This means that it is possible to recognize a completed moult earlier in the moult cycle than an interrupted moult. The frequency of interrupted moult estimated in this study may, therefore, be seen as a minimum value.

As the moult cards available did not cover the beginning of the moult period, they have not been used to estimate moult duration. Furthermore, there were too few within-year recaptures (three) to estimate moult duration reliably from this either. Instead, the 43 days moult duration estimated for Whitethroats by Haukioja (1971) from recapture data has been used to estimate the start and completion dates of moult. The estimation of moult duration from recaptures was used in preference to estimation by linear regression analysis since the latter method often underestimates moult duration (Newton 1966, pers. obs.). The assumption of 43 days moult duration has, for convenience, been used throughout although this ignores the possibility of variation between individuals or through the season (cf. Dolnik & Gavrillov 1980, Noskov & Rymkevich 1985, Hall & Fransson 2000). Assuming 43 days moult duration, the average speed of moult would be 0.7 moult scores per day (a moult score of 30 completed in 43 days). Based on each individual's moult score at capture, the moult speed of 0.7 moult scores per day was used to estimate the individual onset and completion dates of moult. Each day or part of a day was counted as a new day (i.e. 4.1–5.0 days = 5 days).

RESULTS

The extent of interrupted moult

We were able to judge whether moult was interrupted or not in 61 birds. Of these, 43 birds (70.5%) interrupted moult in the secondaries and four (6.6%) in the primaries, giving a total of 77% interrupted moults.

When moult was interrupted in the secondaries, on average 3.7 secondaries were moulted in each wing (left wing: mean = 3.7, range 0–6, $n = 43$, right wing: mean = 3.7, range 0–6, $n = 43$). Two birds completed primary moult but left all secondaries unmoulted. The feather most often left unmoulted was secondary 4 fol-

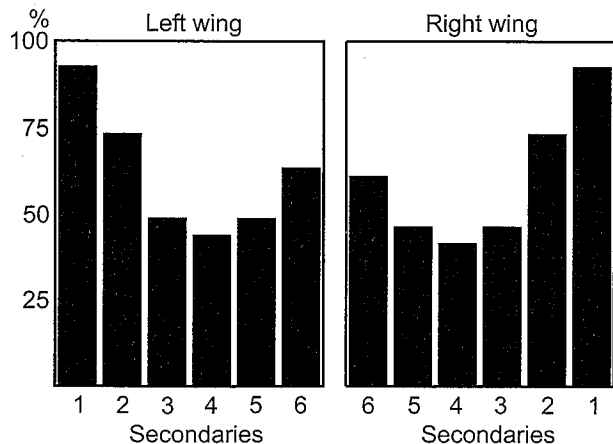


Figure 1. The proportion (%) of different secondary feathers that were moulted among Whitethroats ($n = 41$) interrupting moult in the secondaries but not in the primaries.

lowed by secondaries 5 and 3, with the same pattern in both wings (Fig. 1).

Three out of four Whitethroats interrupting moult in the primaries showed an eccentric moult pattern, leaving some of the central primaries unmoulted. On average 6.5 primaries (range 5–8, $n = 4$) and 1.5 secondaries (range 1–2, $n = 4$) were moulted in the left wing and 7 primaries (range 4–9, $n = 4$) and 1.3 secondaries (range 0–2, $n = 4$) in the right wing. When interruption occurred in the primaries, most often primaries 1–3 and secondaries 5–6 were moulted ($n = 4$). Secondaries 1–4 were never moulted in combination with an interruption in the primaries, but the sample is small (Table 1).

Timing of moult

Assuming a constant moult duration of 43 days for a complete moult (Haukioja 1971), the estimated median date of moult onset was 6 July (range 28 June–21 July) and the estimated date of moult completion was

19 August (range 11 August–3 September) for birds with complete moult ($n = 14$; Fig. 2).

For birds interrupting moult in the secondaries, the median date for starting moult was 17 July (range 3 July–10 August, $n = 23$) and the median completion date was 26 August (range 11 August–11 September, $n = 23$; Fig. 2). If these birds had finished the moult without interruption, the median moult completion date would have been 30 August (range 15 August–22 September).

Birds interrupting moult in the primaries ($n = 4$) gave an estimated median onset date of moult of 10 August (range 27 July–15 August) and completion date of 2 September (range 21 August–10 September; Fig. 2). Had these birds not interrupted moult, the median date of moult completion would have been as late as 23 September (range 9–27 September). One of these individuals was present at a feeding place where migratory fuelling in Whitethroats was studied (Fransson 1998). The bird arrived before moult had started on 1 August, was retrapped in early moult on 9 August, and with interrupted moult on 27 August. Two days later, the bird started migratory fuelling and quickly increased in mass. Moult was estimated to finish on 1 September, and on 3 September the bird left on autumn migration with a fuel load of 60.1% over the lean body mass (body mass 21.7 g; Fig. 3). It is interesting that moult was interrupted in spite of the availability of food at the feeding place.

The estimated date of moult onset differed significantly between the three groups of birds, i.e. with completed moult, with moult interrupted in the secondaries and with moult interrupted in the primaries (Kruskal–Wallis test: $H_2 = 16.71$, $P < 0.001$). Moult completion, on the other hand, was more synchronized and did not differ significantly between groups (Kruskal–Wallis test: $H_2 = 5.31$, ns). For the three moult categories combined the median date of moult completion was 24 August (range 11 August–11 September, $n = 41$).

Table 1. Moulting patterns in four individual Whitethroats interrupting moult in the primaries. 1 = Moulded wing feather; 0 = unmoulted wing feather.

	Left wing:													Right wing:																	
	Primaries						Secondaries						Secondaries						Primaries												
	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	
Bird 1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	0	1	1	1	1	1	
Bird 2	1	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	1	0	0	1	1
Bird 3	0	0	1	1	1	1	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0
Bird 4	1	1	1	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	

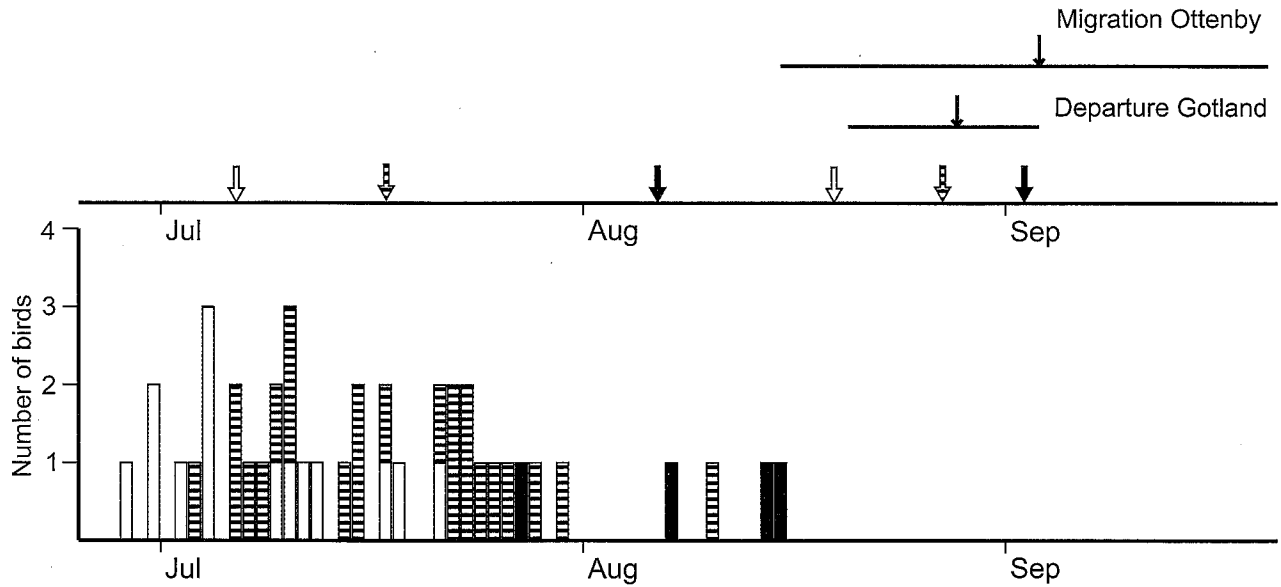


Figure 2. The frequency of estimated onset dates of moult among Whitethroats that completed moult (white), interrupted moult in the secondaries (hatched) and interrupted moult in the primaries (black). Arrows on the line on top of the histogram show median dates of onset (to the left) and completion of moult (to the right). Migration departure dates of adult Whitethroats at Gotland ($n = 8$) and trapping dates of adult Whitethroats on autumn migration at Ottenby ($n = 38$) are shown with range (horizontal line) and median dates (thin arrows).

Moult symmetry

Among birds interrupting moult in the secondaries, 58.5% interrupted moult asymmetrically ($n = 41$), i.e. the number of unmoulted feathers differed between wings (23 birds), or the position of unmoulted feathers differed (one bird). For the 20 of these birds for which we could estimate the moult onset date, this was found to differ significantly between groups (Mann-Whitney U -test: $Z = -2.34$, $n_s = 7$, $n_a = 13$, $P < 0.05$). The median onset date of birds moulting symmetrically (median

9 July, range 6–22 July, $n = 7$) was 14 days earlier than that of birds moulting asymmetrically (median 23 July, range 3–30 July, $n = 13$). Birds were equally likely to have more feathers left unmoulted in the left wing (12 birds) as in the right wing (11 birds), i.e. asymmetry was fluctuating.

Variation within individuals

Four individuals were trapped in more than one year. One of these birds showed an identical interruption of secondary moult in two years (trapped 23 August 1992 and 29 August 1993). Another individual moulted completely in 1991 (29 August) but showed interruption in the secondaries in 1992 (16 August). A third individual had interrupted moult in the secondaries in 1989 (15 August) but had interrupted during primary moult in 1990 (14 August). The fourth bird interrupted moult in the secondaries in all three years but to a varying extent: three (out of 12 possible) secondaries were left unmoulted in 1990 (2 September), ten in 1991 (22 August) and 11 in 1992 (21 August).

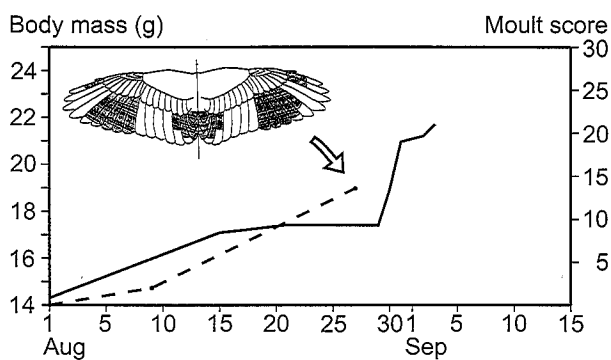


Figure 3. Moulting score (dashed line) and evening body mass (full line) of one Whitethroat at a feeding place on Gotland. The moult card at the last trapping occasion is also shown. Body mass was collected with a remote control balance (for details see Fransson 1998).

DISCUSSION

Interruption of moult and time gain

It is clear from this study that the post-nuptial moult

of Whitethroats breeding in southeast Sweden is not consistent either in the species as a whole or within individuals. The high degree of interrupted moult in the studied population (77%) is similar to that found by Swann and Baillie (1979) among migrants in Crete. Of 99 Whitethroats examined on Crete, 74 birds (75%) had suspended moult in the secondaries. Of these, eight birds (8%) had also suspended moult in the primaries, compared with 6.6% that interrupted primary moult in our study. It is possible that some of the birds trapped in Crete were of Swedish origin because several Swedish ringed birds have been recovered in Greece, Libya and Egypt in autumn (Stockholm Bird Ringing Centre, unpublished). Two Swedish ringed birds have also been recovered in the winter quarters in southern Chad, one in November and the other in February.

Pimm (1973) estimated that about 39% of British Whitethroats had the opportunity to interrupt secondary moult, since this was the proportion of birds finishing secondary moult after primary moult had been completed. He also found that 40% (out of 64 birds) of the Whitethroats trapped by him in Coto Doñana, Spain, in 1967 had interrupted post-nuptial moult. In the Gotland population the degree of interruption was higher, with a later date of moult onset. In other words, moult can be adjusted to end within a certain time interval. The onset of moult was 25 days later for Whitethroats interrupting primary moult compared to those that interrupted in the secondaries, and up to 36 days later than birds that completed moult (Fig. 2). The interruption of moult reduced the time difference between the groups, and moult completion was more synchronized among the groups compared to the onset. Birds interrupting in the primaries completed moult only 7 days later than birds interrupting in the secondaries, and no more than 14 days later than birds with complete moult (Fig. 2).

In several species, the moult performance of individual birds is regulated by photoperiod (e.g. Dolnik & Gavrillov 1980, Moore *et al.* 1982, Noskov & Rymkevich 1985, Dawson 1998, Hall & Fransson 2000), and it is reasonable to believe that this is also true of the Whitethroats in this study. The Whitethroat's moult on Gotland is performed during a period when the change in daylength is significant; decreasing by 2 h 19 min through August alone.

Asymmetry and flight performance

It seems likely that the higher degree of asymmetrical moult seen later in the season may be caused by time-

stress. Parsons (1990) showed that various stress factors could increase the degree of fluctuating asymmetry, and Witter and Lee (1995) showed that in Common Starlings *Sturnus vulgaris* asymmetry in the length of primary feathers increased with the stress of higher perceived predation risk during moult. Møller (1997) pointed out that asymmetrical individuals often have a higher metabolic rate than symmetrical individuals. Thus asymmetrical moult might be symptomatic of an increase in metabolic rate caused by the stress of moulting late. It is not clear, however, whether fluctuating asymmetry is a good measure of stress or not (Bjorksten *et al.* 2000).

Considering flight mechanics, we should expect asymmetry caused by unevenly abraded feathers, and an unequal number of abraded feathers in the wings, to be detrimental. Abraded feathers also reduce wing-area, and abraded wing tips would reduce wing-span. An area reduction of the tips of the outermost primaries has been shown to have a detrimental effect on the generation of lift in the Ruby-throated Hummingbird *Archilochus colubris* (Chai 1997). In this study it is interesting that three out of four Whitethroats interrupting moult in the primaries retained some central primaries but moulted the primaries at the wing tip.

Synchronized migration

The dates of moult completion of both complete and interrupted moults in this study correspond well with the autumn migration departure dates of Whitethroats in southern Sweden. Fransson (1998) estimated the median migration departure date of adult Whitethroats in our study population to be 27 August (range 20 August–3 September, $n = 8$, Fig. 2). At Ottenby Bird Observatory (56°12'N 16°24'E), about 135 km west-southwest of the trapping site at Gotland, the trapping of adult Whitethroats (of unknown origin) on autumn migration peaks at 5 September (range 1 August–29 September, $n = 38$, unpubl. data 1978–90; Fig. 2). The synchrony of moult completion, and the correspondence between the median dates of moult completion and autumn migration departure suggest an optimal migration departure date.

It is not yet understood why an early onset of migration is important. Pimm (1973) suggested that interrupted moult was an adaptation to unpredictable weather conditions in Britain at the end of the breeding season. However, it appears that the environmental conditions on Gotland are still favourable when migra-

tion begins. Data from the individual moulting at the artificial feeding site also support the argument that food availability does not affect the decision to interrupt moult. It is therefore more plausible that selection favours early arrival in the winter quarters. An early arrival on the winter grounds might be important to secure a winter territory. Little is known about winter territoriality of Whitethroats, but Brosset and Erard (1977) noticed a Whitethroat occupying a territory in Gabon in January, and winter territories are known to be held by other Palearctic migrants such as the Greenish Warbler *Phylloscopus trochiloides* (Price 1981).

In Africa north of the Equator, where *S. c. communis* spend the winter, the northward movement of the inter-tropical rain front coincides with the northern summer (Hogg *et al.* 1984, Aidley & Wilkinson 1987). Because of this, food is abundant in September and October but declines from November onwards (Hogg *et al.* 1984). It may therefore be important to cross the Sahara Desert before the southern edge of the desert has become dry, because once the dry season commences, the desert crossing will be extended by 400–600 km (Hogg *et al.* 1984). This distance equates to one or two nights of flight, and a need for a disproportionate extra fuel load since the distance gained per unit of fuel decreases with increasing fuel load (Alerstam & Lindström 1990).

The importance of arriving early at winter sites is supported by the fact that late migrating *Sylvia* warblers migrate faster than early migrating birds (Fransson 1995). Alerstam and Lindström (1990) also concluded that time might be an important factor in long-distance bird migration. With an overall autumn migration speed of 96 km/day (Fransson 1995), adult Whitethroats breeding on Gotland would reach their winter quarters in, for example, Chad or Sudan in 50–55 days, i.e. at the end of October. The main passage through Central Sudan is also found to occur in October (Hogg *et al.* 1984).

The results of this study indicate that the post-nuptial moult in Whitethroats may be interrupted on the breeding grounds in order to allow autumn migration before a critical date. The early migration to winter quarters may facilitate the Sahara crossing by shortening the distance over inhospitable areas by one or two nights of flight.

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