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Lesser whitethroats *Sylvia curruca* under time constraint do not interrupt moult

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Using a more severe time constraint, this study repeats a previous experiment to investigate how lesser whitethroats *Sylvia curruca* handled a situation of time-constraint during wing moult, and especially to see whether they showed interrupted moult. Twenty-eight lesser whitethroats were trapped during spring migration and kept in the laboratory until the end of moult. During moult the light regime was manipulated in order to impose a time-constraint on half of the birds. In spite of the greater time-constraint in the present study the results were similar to those found earlier, with a shorter moult duration and wing length in the time-constrained groups. Moult duration differed by 7.9 days between treatment groups in the present study and by 6.2 days in the earlier experiment. Most surprisingly, interrupted moult did not seem to be a normal strategy for lesser whitethroats even under severe time-pressure. Two birds (out of 28) interrupted moult, but one of them belonged to the control group. The similar results between the two years further indicated a lower limit around 40 days for uninterrupted moult. In both studies the experimental birds started to moult 11 days after the manipulation of day length. Eleven days is, thus, probably the time needed for the body to respond and adapt to the new environmental conditions.
Key words: moult, interrupted moult, time-constraint, *Sylvia*, wing length.

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In 1999 Hall and Fransson (2000) performed an experiment investigating how lesser whitethroats *Sylvia curruca* handled a situation of time-stress during moult. A time-constraint was induced on the birds through manipulating day length. The lesser whitethroats responded to the manipulation by adjusting moult performance in several ways (Table 1) and, due to these adjustments, all time-constrained birds finished moult within the normal time span for lesser whitethroats in Sweden (Fig. 1). A surprising result was that only one bird interrupted moult, though the species is known to interrupt moult occasionally in Russia (Stolbova & Muzaev 1990). By comparison, Hall and Fransson (2001) found that moult interruptions in common whitethroats *Sylvia c. communis* occurred more frequently the later moult began, indicating a higher proportion of interruptions under increased time-constraint. Interrupted moult probably caused by time-constraint has also been reported for willow warblers *Phylloscopus trochilus* (Bensch et al. 1985, Hedenström et al. 1995).

The aim of the present study was to find out whether a higher proportion of lesser whitethroats would interrupt moult if a more severe time-constraint were imposed upon them than in the earlier experiment.

Methods

The experiment was conducted at Tovetorp Zoological Research Station (58°56'N, 17°08'E) in southeast Sweden during May to August 2000. Twenty-eight lesser whitethroats were trapped in May during spring migration at Landsort Bird Observatory (56°45'N, 17°52'E), and transported to the laboratory at Tovetorp.

At Tovetorp the birds were kept in separate cages (52 x 52 x 70 cm) in four rooms maintained at about 20 °C. Individuals were placed in the cages at random and the cages were separated by cloth to prevent the birds from seeing each other. Daylight illumination came from sunshine-simulating fluorescent tubes, and dawn and dusk light (30 min before to 30 min after daylight) was from electric bulbs. The daylight was turned on and off in two steps with 10 minutes delay. The first day a moulted remex was found (June 16) the light regime in two of the rooms (from here on called the time-constrained) were changed in order to impose a time-constraint. In the two time-constrained rooms the light regime was switched to one that was 60 days ahead of the control rooms, thereby transferring the birds to the day length of 16 August (in the previous study they had been transferred to the daylength of 2 August). The light regime in the control rooms followed the normal light regime of the Stockholm area. The birds were first checked for moult at the latest one day after the first remex was shed, and on this occasion the birds were sexed, based on the occurrence (female), or lack of (male), an incubation patch (Svensson 1992). For further details on trapping and housing conditions see Hall & Fransson (2000).

Moult was scored according to Sondell's (1977) method in which the length of each growing feather is estimated to the nearest one-tenth of its full-grown length. Moult was recorded on separate moult cards on several occasions during the moult period. When moult was completed the birds were released at Tovetorp. Primaries were numbered descendantly, from the carpal joint outwards and secondaries were numbered ascendantly from the middle of the wing inwards towards the body. The short primary ten was not considered in this study. All mean values are presented ± s.e.

Results

Birds from the four rooms did not differ in mean wing length at trapping (66.6 ± 0.42 mm, 66.6 ± 0.57 mm, 66.8 ± 0.60 mm, 67.0 ± 0.62 mm; ANOVA: $F_{3,24} = 0.12$, n.s.).

The median date of moult onset differed by seven days between treatments (control birds 4 July, time-constrained birds 27 June; Mann-Whitney U-test: U = 20.5, $n_c = n_t = 14$, P < 0.01, Table 1). For the time-con-

Table 1. Summarised data for lesser whitethroats kept under normal day length (control birds) and shortened day length (time-constrained birds) in 1999 (day length shortened by 40 days) and 2000 (day length shortened by 60 days). Data for 1999 from Hall & Fransson (2000).

	Actual dates			
	control	range	time-constrained	range
1999				
Moult onset date	6 July	23 June–13 July	4 July	27 June–13 July
Moult completion date	21 August	11–29 Aug	14 August	7–17 August
Moult duration	47.1 days	37–57 d	40.9 days	31–47 d
Duration without interruption			41.6 days	37–47 d
No. of growing remiges	14.1	8–19	18.0	12–22
Wing length	+1.2 mm		– 0.8 mm	
2000				
Moult onset date	4 July	16 June–25 July	27 June	21 June–3 July
Moult completion date	21 Aug	11–31 Aug	5 Aug	30 July–11 Aug
Moult duration	47.8 d	29–56 d	39.9 d	37–42 d
Duration without interruption	49.3 d	46–56 d	39.8 d	37–42 d
No. of growing remiges	13.1	9–17	18.5	15–23
Wing length	+0.7 mm		+0.3 mm	

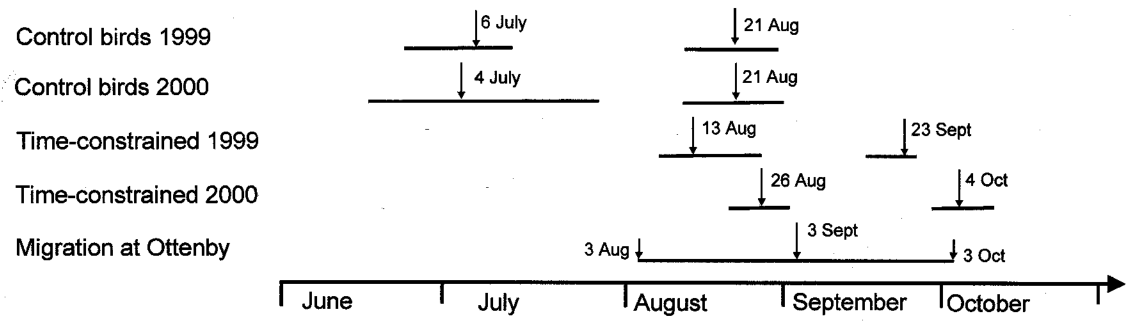

Figure 1. Experienced dates of moult onset (left) and completion (right) of lesser whitethroats in the laboratory at Tovetorp Zoological Research Station 1999 and 2000. Range (horizontal lines) and median dates (arrows) are shown. Autumn migration departure dates of adult lesser whitethroats at Ottenby, SE Sweden, are also shown with range (horizontal line and short arrows) and median dates (long arrow). Data for 1999 from Hall & Fransson (2000).

strained birds the experienced median date of moult onset was 26 August (Fig. 1).

Mean moult duration did not differ between the two control groups (46.7 ± 3.1 d cf. 48.9 ± 1.6 d, $t_{12} = -0.62$, n.s.) or between the two time-constrained groups (40.0 ± 0.8 d cf. 39.7 ± 0.5 d, $t_{12} = -0.31$, n.s.). The two control groups and the two time-constrained groups were therefore pooled in further analyses. Mean moult duration differed by 7.9 days between treatments (control 47.8 ± 1.7 d, time-constrained 39.9 ± 0.4 d, $t_{26} = -4.5$, $P < 0.01$, Table 1).

The median date of moult completion differed by 16 days between treatments (control birds 21 August, time-constrained birds 5 August; Mann-Whitney U-test: $U = 0.5$, $N_c = N_t = 14$, $P < 0.001$). The experienced median date of moult completion for the time-constrained group was 4 October (Fig. 1).

Both moult onset and moult completion were more synchronised among time-constrained birds than among control birds (range of onset: time-constrained 12 days, control 39 days, F-test: $F_{13,13} = 8.18$, $P < 0.05$; range of completion: time-constrained 12 days, control 20 days, F-test: $F_{13,13} = 2.98$, $P < 0.05$). Within each treatment group moult onset and moult completion were equally synchronised; F-test: time-constrained $F_{13,13} = 1.19$, n.s., control $F_{13,13} = 2.31$, n.s.).

Out of 30 wing feathers (9 primaries and 6 secondaries on each wing), time-constrained birds grew more feathers simultaneously (18.5 ± 0.64 feathers, range 15–23, n = 14) during the most intense growth period (about 24 days from start), than did control birds (13.1 ± 0.78 feathers, range 9–17, n = 14, $t_{26} = 5.31$, $P < 0.01$; Table 1).

Two birds interrupted moult: one control bird and one time-constrained bird. In both cases it was the last individual to start moult within each treatment group (onset date for control 25 July; time-constrained 3 July, corresponding to 1 September) and both interruptions

Table 2. Moult patterns in three lesser whitethroats interrupting moult, one time-constrained bird in 1999 and one time-constrained and one control bird in 2000. 1 = moulted 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
time-constr. 1999	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1
time-constr. 2000	1	1	1	1	0	0	0	1	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	0	0	0	1	1	1	1
control 2000	1	1	1	1	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	1

were eccentric (Table 2). In both cases the interruptions gave shorter moult duration compared to the average moult duration of the other birds in the same treatment group, although only very slightly so in the time-constrained bird (control: 29 days compared to 49.2 ± 1.0 days, time-constrained: 39 days compared to 39.9 ± 0.5 days).

At the time of release wing lengths had increased compared to time of trapping in the control group (trapping: 66.8 ± 0.41 mm, cf. release: 67.5 ± 0.42 mm; paired t-test, t_{13} = 2.9, $P < 0.05$), but not in the time-constrained group (trapping: 66.7 ± 0.35 mm cf. release: 67.0 ± 0.34 mm; paired t-test: t_{13} = 2.0, n.s.; Table 1).

Discussion

The median date of moult onset differed between treatments in the present experiment in 2000 (control: 4 July, time-constrained: 27 June) but not in the earlier study in 1999 (control: 6 July, time-constrained: 4 July). In both years, the birds under induced time-constraint started to moult after the same time had passed since manipulation of the daylight regime (11 days), probably reflecting the time needed for the body to respond and adapt to the new environmental conditions. The change in time regime was induced seven days earlier in 2000 (16 June) than in 1999 (23 June). It is therefore reasonable to believe that the discrepancy between years is explained by the earlier introduction of the change in time regime in 2000.

Moult intensity was similar between the two years within each treatment group. Control birds grew on average 13–14 feathers simultaneously during the most intense period of moult and the time-constrained birds grew on average 18–19 feathers (Table 1). This might indicate an upper limit, around 18–19 feathers to be grown simultaneously, above which the reduced wing area would so severely reduce flight ability (Haukioja 1971, Tucker 1991, Swaddle & Witter 1997) that moult speed may be limited by decreased foraging ability. The lower number, 13–14 feathers growing simultaneously, might indicate the most favourable trade-off between moult speed and flight ability.

The average moult duration was significantly shorter among time-constrained birds than among controls in both years (1999: t_{26} = –3.5, $P < 0.01$, 2000: t_{26} = –4.5, $P < 0.01$), but within treatments moult duration did not differ between 1999 and 2000 (time-constrained: t_{26} = 0.84, n.s.; control: t_{26} = –0.29, n.s.; Table 1). As with moult intensity 47–48 days might indicate the most favourable trade-off between moult duration and flight ability and 40 days the shortest possible moult duration without interruptions. Evidently, lesser whitethroats do not moult at maximum speed during normal conditions, probably because a reduced flight ability does not only increase the cost of flight itself, but also decreases foraging efficiency and enhance the risk of being caught by predators.

The dates of moult completion experienced by time-constrained birds in 1999 ranged from 16 to 26 September (median 23 September, n = 14; Fig. 1). Under the more severe time-constraint in 2000 the corresponding experienced dates of moult completion ranged from 28 September to 10 October (median 4 October, n = 14). In 1999 all birds completed moult in time to migrate within the normal autumn migration period but in 2000 some of the time-constrained birds completed moult too late for this (Fig. 1). This indicates that although lesser whitethroats can compensate for a late moult onset there is a limit to the adjustability of moult. Interestingly the severe time-constraint did not lead to interrupted moult or birds not moulting at all.

In 1999 the time-constrained birds decreased their wing length by an average 0.8 mm between the time of trapping and their release after moult. In contrast, control birds increased their wing length by 1.2 mm on average, giving a mean difference in wing length of 2 mm between the two treatment groups (Table 1). A similar result was found by Dawson et al. (2000) in an experiment with starlings *Sturnus vulgaris*. The starlings kept under shortened day length grew primary feathers that were 3 mm shorter than the birds kept on a longer day length. In 2000 the wing length of the time-constrained lesser whitethroats in this study did not change significantly, but the control birds increased the wing length by 0.7 mm. Thus, as in 1999 there was a tendency towards a shorter wing length among time-constrained birds compared to control birds. The reasons for the discrepancy between 1999 and 2000 are unknown.

Only one time-constrained bird interrupted moult in 1999 and, despite the more severe time-constraint imposed upon the birds in 2000, the proportion of birds showing interrupted moult did not change. While the predisposition to interrupt moult may vary between individuals and at least some of the lesser whitethroats in Sweden have this ability, it is rarely observed in nature. This study confirms the earlier finding that it is not a normal strategy for moult adjustment in lesser whitethroats.

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