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Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers

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Migrating passerines moulting in the breeding quarters before autumn migration sometimes end up with less time than needed for a normal moult. To deal with this the birds could for example suspend moult or moult faster. In this paper we investigate the effect of an induced time-constraint on the moult of Lesser Whitethroats Sylvia curruca. The time-constraint was induced through a shift in light regime large enough to transfer the birds to a date when, under normal conditions, they already should have started moulting. Time-constrained birds moulted faster and also grew shorter wing feathers, resulting in a shorter wing, compared to control birds. Only one individual responded by interrupting moult and retained a number of inner primaries unmoulted. The observed adjustments of moult, and the higher fuel loads towards the end of moult, are consistent with the ideas that time is an important factor in bird migration, affecting not only migration but also the events preceding it.

Birds have to moult their feathers within certain intervals due to abrasion. With only a few exceptions all Western Palaearctic passerine migrants moult their flight feathers annually (e.g. Svensson 1992). This is most often done as a post-nuptial moult, after breeding and before autumn migration. As the time available can vary due to the timing of breeding, birds with post-nuptial moult sometimes end up with less time than needed for a normal moult. As moult impairs flight ability (Swaddle and Witter 1997) it is important not to be in moult during long-distance migrations. A few strategies are known to deal with this time-constraint. The moult can for example be interrupted or suspended (e.g. Mead and Watmough 1976, Swann and Baillie 1979, Hedenström et al. 1995), in the latter case to be resumed in the winter quarters. In a breeding population of Whitethroats Sylvia communis on Gotland, SE Sweden, 77% of the birds suspended moult (K. S. S. Hall and T. Fransson unpubl.). The Barred Warbler Sylvia nisoria shows a special moult strategy, the split-moult, which may be an adaptation to deal with time pressure (Hasselquist et al. 1988, Lindström et al. 1993). In the split-moult some flight feathers are moulted in the summer quarters after breeding and the remaining ones on the winter grounds. The split-moult resembles suspended moult but the moult sequence starts already in the birds' first winter. If the suspended, interrupted and split-moult systems are strategies to avoid time pressure, the optimal solution might be a complete moult in the winter quarters, after migration. Winter moult is, in

accordance with this, a common pattern among the most long-distance migrating, and thereby probably the most time-constrained, species (e.g. Jenni and Winkler 1994, Norman 1997). Svensson and Hedenström (1999) also showed that winter moult probably is the evolutionarily most recent moult strategy and suggested that split-moult may be an evolutionary intermediate state between summer and winter moult. Another strategy to deal with time-constraints is to moult faster. Haukioja (1971) reported moult so intensive as to cause flightlessness in northern populations of Whitethroats, Bluethroats *Luscinia svecica* and Willow Warblers *Phylloscopus trochilus*. A higher moult speed may be accomplished by a faster growth of feathers or by growing more feathers simultaneously.

The annual cycle of many migratory birds has been shown to rely on an endogenous rhythm organising events such as reproduction, moult and migration (e.g. Gwinner 1996). The circannual clock is species- or population-specific and seems to be synchronised by environmental cues such as photoperiod, a fact that has been used to experimentally manipulate moult performance (Dolnik and Gavrilov 1980, Moore et al. 1982).

The aim of this study was to investigate how the Lesser Whitethroat *Sylvia curruca* deals with a time-constraint during moult. Lesser Whitethroats breeding in Sweden migrate to wintering areas in East Africa (Moreau 1972). They are, in contrast to Whitethroats, not known to suspend moult in Sweden (Svensson 1992, own obs.) but suspended moult has been reported occasionally from Russia (Stolbova and Muzaev 1990). One question that we wanted to investigate was whether Lesser Whitethroats breeding in Sweden can react on a severe time-constraint by suspending moult, in spite of the rarity of this pattern.

Methods

The study was conducted at Tovetorp Zoological Research Station (58°56′N, 17°08′E) in SE Sweden. A total of 28 Lesser Whitethroats were mist-netted during May 1999 before breeding was likely to have started and were transferred to the laboratory. Of these birds, 15 were trapped at Landsort Bird Observatory (58°45′N, 17°52′E), three birds were trapped at Torö (58°48′N, 17°52′E), and the remaining ten were trapped in the surroundings of Tovetorp. At capture the birds were ringed, aged, weighed and their wing length was measured. Ageing followed Svensson (1992) and wing length was measured to the nearest mm according to method 3 (flattened and straightened wing, Svensson 1992).

The birds were kept in separate cages (70 × 52 × 52 cm) in four rooms, with seven cages in each room. Individuals were placed in the cages at random, and cages were separated by cloth giving the birds no

possibility to see each other. Most of the birds were in their second year of life and only three birds in each treatment were assigned as older. The birds had free access to vitamin-enriched water and a dry food mixture similar to the one described by Berthold et al. (1990). About 50 g of dried insects was added per kilo dry food mixture. The birds had free access to mealworms *Tenebrio molitor* during the first days in captivity, but this amount was decreased successively to 2 g a day. Occasionally a few black-current berries *Ribes nigrum* were also given to the birds. Room temperature was about 20°C. Daylight illumination came from sunshine-simulating fluorescent tubes, and dawn and dusk light (30 min before and after daylight) from regular electric bulbs. The light regime followed the normal day length for the Stockholm area in all rooms until the start of the experiment.

On 23 June the light regime in two rooms, randomly chosen, was changed to resemble that on 2 August. From this date on, these rooms (from now on called the time-constrained) followed a light regime of dates 40 days later than that of control rooms. This exposed the time-constrained groups of birds to a day length corresponding to a date when they already should have started moulting under normal conditions. Based on a moult card material from Gotland (56°55′N, 18°8′E) (Sundre Bird Ringing Group unpubl.), moult was estimated to start between 5 July and 16 August (median 21 July, N = 39), by assuming a moult duration of 40 days (Ginn and Melville 1983). The shift in light regime was made on the first day a shed flight feather was found. As this bird, by chance, ended up in the control group it has been included anyhow. Four days after the shift in light regime the first bird from the time-constrained group started moulting.

Moult of primaries and secondaries was recorded according to Sondell's (1977) method in which the length of each new feather is estimated to the nearest 10th of its full-grown length. The minute outermost primary and the tertials were not considered so a bird which had completed moult obtained a moult score of 30 (nine primaries and six secondaries on each wing). Primary feathers were numbered descendantly and secondaries ascendantly.

The cages were checked for shed remiges every second day and the first day a dropped flight feather was found was considered the bird's start of moult. To minimise handling effects on moult performance, moult progress was checked as few times as possible. Moult was checked for the first time ten days after the first dropped wing feather was found, and thereafter at 24 days, 34 days and as close to completion as possible. When moult was completed the birds were released at Tovetorp. Each time the moult was checked the birds were also weighed on an electronic precision balance to the nearest 0.1 g. Before release wing length was once again measured. When released the birds were all in

good condition and none showed any sign of fault bars or other plumage deficiencies.

To estimate release fuel loads (in % of lean body mass) the lean body mass of each bird was estimated from wing length at capture and the size-specific lean body masses estimated for Lesser Whitethroats by Ellegren and Fransson (1992). All mean values are presented $\pm$ SE.

Results

Birds from the four rooms did not differ in mean wing length at trapping ($\bar{x}_1 = 65.4 \pm 0.3$ mm, $\bar{x}_2 = 66.6 \pm 0.5$ mm, $\bar{x}_3 = 66.1 \pm 0.5$ mm, $\bar{x}_4 = 66.0 \pm 0.7$ mm; ANOVA: $F_{3,24} = 0.9$, NS).

The median date of onset of moult did not differ between treatments (control birds 6 July, range 23 June–13 July, and time-constrained birds 4 July, range 27 June–13 July; Mann-Whitney U-test: $U = 86.5$, $N_c = N_t = 14$, NS). For the time-constrained birds the experienced median date of onset was 13 August.

Mean moult duration did not differ between the two control groups ($\bar{x}_1 = 47.1 \pm 2.0$ d, $\bar{x}_2 = 47.1 \pm 2.1$ d, $t_{12} = 0.0$, NS), or between the two time-constrained groups ($\bar{x}_3 = 39.0 \pm 1.6$ d, $\bar{x}_4 = 42.7 \pm 1.3$ d, $t_{12} = 1.8$, NS), respectively. Thus, the two control groups and the two time-constrained groups were pooled in the following analyses.

Mean moult duration differed by 6.3 days between treatments ($t_{26} = 3.5$, $P < 0.01$), with a longer moult duration in control birds ($\bar{x}_c = 47.1 \pm 1.4$ d, range 37–57 d, $N = 14$) than in time-constrained birds ($\bar{x}_t = 40.9 \pm 1.1$ d, range 31–47 d, $N = 14$). (By excluding one bird not performing a complete moult the mean moult duration of the time-constrained group was 41.6 days, range 37–47 d.) Within both treatments moult duration was shorter with later onset date, significantly so, however, only in the time-constrained group (Spearman rank correlation: controls $r_s = -0.5$, $N = 14$, $P = 0.07$, time-constrained $r_s = -0.7$, $N = 14$, $P < 0.05$).

The median date of moult completion differed between treatments (control 21 August, range 11–29 August, time-constrained 14 August, range 7–17 August, Mann-Whitney U-test: $U = 31.0$, $P < 0.01$). The median date of moult completion for time-constrained birds, 14 August, corresponds to the experienced date of 23 September (range 16–26 September). Moult completion was also more synchronised among time-constrained birds (range 10 days) than among control birds (range 18 days) (F-test: $F_{1,26} = 3.6$, $P < 0.05$).

Out of 30 wing feathers (9 primaries + 6 secondaries on each wing) time-constrained birds grew more feathers simultaneously ($\bar{x}_t = 18.0 \pm 0.9$ feathers, range 12–22, $N = 14$) during the most intense growth period (24 days from start) than did control birds ($\bar{x}_c = 14.1 \pm 0.8$ feathers, range 8–19, $N = 14$, $t_{26} = -3.2$, $P < 0.01$).

The last bird to start moult in the time-constrained group retained the inner primaries and started moult at primary 6 on the right wing, and at primary 5 on the left wing. From this start the moult advanced as normal and was completed in both primaries and secondaries in a manner expected of a normal complete moult, except the 9 unmoulted innermost primaries. This resulted in the shortest moult duration of all individuals (31 days).

At release the change in wing length compared with trapping in spring differed between treatments. Mean wing length had increased by 1.2 mm in the control group (trapping: $\bar{x}_c = 66.0 \pm 0.3$ mm, release: $\bar{x}_c = 67.2 \pm 0.4$ mm. Paired t-test: $t_{13} = 3.8$, $P < 0.01$), and decreased by 0.8 mm in the time-constrained group (trapping: $\bar{x}_t = 66.1 \pm 0.4$ mm, release: $\bar{x}_t = 65.3 \pm 0.3$ mm. Paired t-test: $t_{13} = -2.5$, $P < 0.05$) (Fig. 1). At release wing length thus differed by nearly 2 mm between treatments ($t_{26} = 4.3$, $P < 0.001$). The change in wing length was positively correlated with moult duration (Spearman rank correlation: $r_s = 0.5$, $P < 0.01$, $N = 28$). Analysing each treatment group separately, there was a positive correlation within the control group ($r_s = 0.5$, $P < 0.05$, $N = 14$), but not within the time-constrained group ($r_s = -0.1$, NS, $N = 14$).
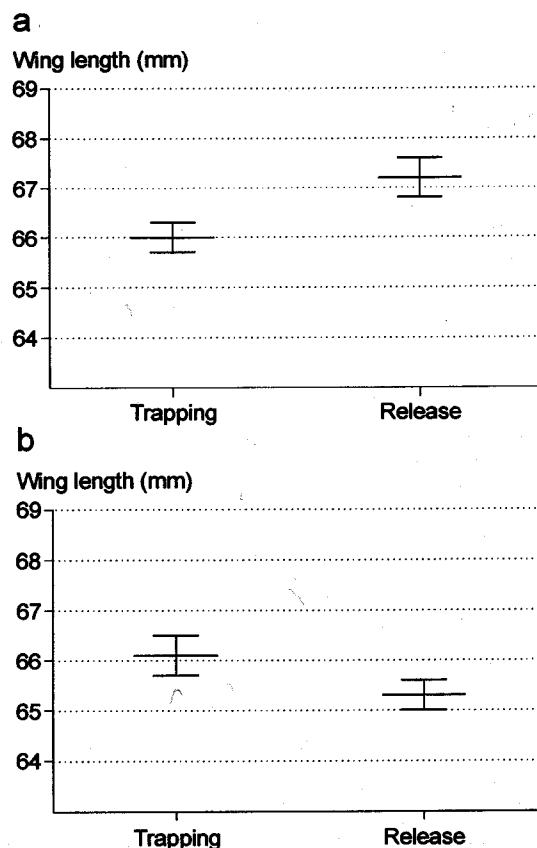

Fig. 1. Wing length (mean $\pm$ SE) in the Lesser Whitethroats on the trapping and release occasions. (a) Control birds, (b) time-constrained birds.

The time-constrained birds had higher average fuel load ($\bar{x}_t = 24.0 \pm 2.5\%$ of lean body mass, $N = 14$, range 12.4–47.6%), when released, than did control birds ($\bar{x}_c = 17.5 \pm 1.9\%$ of lean body mass, $N = 14$, range 4.0–25.2%, $t_{26} = 2.1$, $P < 0.05$).

Discussion

In this study time-constrained Lesser Whitethroats did not, in general, respond to the time pressure by suspended moult, but instead moulted faster and grew shorter wings than control birds. This is in accordance with findings that late moulting adult Great Tits *Parus major* grew shorter wings than earlier moulting individuals (Dhont 1981). Dhont suggested the shorter wings might be the price paid for having invested in a second brood, i.e. the natural way to end up with a time-constraint. In this study it was evident that the change in wing length was correlated with moult duration under normal conditions. The lack of correlation within the time-constrained group is unexpected but can be a result of the fact that the variation in moult duration was rather small and that a majority of the birds grew a shorter wing. It also indicates that the shorter moult duration observed in this group was a result not only of growing shorter wing feathers but also of a generally faster moult, which the higher number of simultaneously growing wing feathers shows.

One cost of having shorter wing feathers may be an impaired flight performance due to the reduced wing area and thereby increased wing loading (Kullberg et al. 1996, Swaddle and Witter 1997, Lind et al. 1999). A reduced wing area might affect foraging efficiency and increase predation risk (Slagsvold and Dale 1996). It has also been suggested that there is a positive relationship between relative wingspan and migration speed (Hedenström and Alerstam 1998). A shorter wing, in this case reducing wing span by 4 mm, might prolong the autumn migration period.

A faster moult as a response to shortened day length has previously been shown in for example Chaffinches *Fringilla coelebs* (Dolnik and Gavrilov 1980) and White-crowned Sparrows *Zonotrichia leucophrys gambelii* (Moore et al. 1982). In an experiment with Bluethroats Lindström et al. (1994) found no response in moult speed to a shortened day length. They suggested the Bluethroats already moulted as fast as possible or that the change in light regime came too late. In contrast to that study the change in light regime in the present study was done as close to start of moult as possible and this gave several responses among the Lesser Whitethroats. For the birds to respond to the shorter day length by adjusting moult performance, it is probably also important that the time shift transfers the birds to a date well beyond the date of moult start under natural conditions. In addition, Dawson (1998),

in an experiment with photoperiodic control mechanisms in House Sparrows *Passer domesticus*, showed that a decrease in day length after the onset of gonadal regression increased moult speed, whereas a decrease before gonadal regression began did not.

The median trapping date of adult Lesser Whitethroats on autumn migration at Ottenby, SE Sweden (56°12′N, 16°24′E), during the period 1978–90 was 3 September with a range from 3 August to 3 October (N = 143) (Ottenby Bird Observatory unpubl.). The moult completion for the time-constrained birds in the present study was thus within the normal range of autumn migration departures at Ottenby, although among the latest. The smaller range in completion of moult, among time-constrained compared to control birds, might indicate that an optimal departure date exists and that the time-constrained birds were able, at least partly, to handle the encountered situation.

Both treatment groups seem to have started moult earlier than normal but this is probably a result of not being able to breed. A tendency towards earlier onset of moult among captive birds unable to breed has previously been reported by, e.g., Newton (1967) for Bullfinches *Pyrrhula pyrrhula* and Greenfinches *Carduelis chloris* and by Dhont (1973) for Great Tits *Parus major*.

According to Svensson (1992) the post-breeding moult of the Lesser Whitethroat is complete, but in Russia occasionally Lesser Whitethroats have left some secondaries unmoulted (Stolbova and Muzaev 1990). The only individual in this study that showed any kind of interruption of moult retained the innermost primaries but finished moult of both primaries and secondaries as expected in a normal complete moult. This kind of partial primary moult has previously been reported as eccentric and found in other *Sylvia* species, but not, to our knowledge, in Lesser Whitethroats (cf. Jenni and Winkler 1994). Why the time-constrained Lesser Whitethroats in this study did not show any suspension of secondary moult, in contrast to the Whitethroat population on Gotland (K. S. S. Hall and T. Fransson unpubl.), remains to be investigated. Maybe the differences in breeding performance between the two species are large enough to account for the different strategies.

The time-constrained birds had higher fuel loads than control birds when released, in accordance with the results of Lindström et al. (1994) for Bluethroats under similar experimental conditions. Moore et al. (1982) also obtained similar results when manipulating light regimes during moult in White-crowned Sparrows. A higher fuel load makes it possible to leave on migration sooner and provides fuel for a longer initial migratory journey.

The observed adjustment of moult in relation to time of season in Lesser Whitethroats makes it possible, at least partly, for an individual to compensate for being late and to depart on migration earlier than otherwise

would have been possible. The higher fuel load observed, close to the completion of moult in time-constrained birds, might further advance the migratory departure. These findings are consistent with the ideas that time is an important factor in bird migration (cf. Lindström and Alerstam 1992) affecting, as shown in this study, not only the actual migration but also events preceding it.

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