

Post-nuptial moult variation in the Willow Warbler *Phylloscopus trochilus* in relation to breeding

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In a nine-year study of post-nuptial moult interruption in the Willow Warbler, three moult patterns were noted which differed from the normal pattern. All concerned late-breeding individuals. One pattern was to suspend moult after the first two inner primaries were renewed and recommence at the point of suspension when young had attained independence. Another pattern was a very slow renewal of inner primaries with adjacent feathers only dropped when previous ones were fully grown and subsequently proceeding into a full moult when young were independent. In the third pattern, birds commenced their moult at an earlier stage of the breeding cycle, i.e. before young were independent. In all three patterns, post-nuptial moult would be completed earlier than if all birds waited until young achieved independence before moult was initiated, as is usually the case in adults with normal-timed broods.

Many factors influence the timing, duration and extent of post-nuptial moult in trans-Saharan migrants, and some overlap occurs between moult, breeding and migration.^{1–7} In the family *Sylviidae*, around half of the species postpone their full moult until after migration south.⁸ Some, principally summer moulting species, show adaptive variations^{9–13} and it has been suggested that some species, such as the Barred Warbler *Sylvia nisoria*, may be in the process of changing their moult season from summer to winter.¹ These adaptations may be the result of species-specific time constraints in the period after breeding has finished, which either restrict the completion of a full moult before migration takes place,¹² or birds delay the full moult until winter quarters are reached.⁸

The start of moult also varies within populations according to an individual bird's breeding condition and/or geographical breeding area.⁸ Usually, early breeders moult before late breeders and more southern populations before more northern ones.^{14–16} A sex difference in the timing and duration of moult can also occur

with males usually starting before females.^{2,4,5,16} Suspension of post-nuptial primary moult during breeding in England has been recorded in the Willow Warbler.¹⁷ An interruption of secondary moult occurred in 5% ($n = 250$) of the *trochilus* race studied in Iberia during autumn migration¹⁸ with a much higher incidence in the *acredula* race studied in Crete (9%, $n = 450$)¹⁹ and Russia (8–21%, $n = 408$).²⁰ These more northern populations of Willow Warblers (i.e. north of 60°N) are also more prone to start moult at an earlier stage of the breeding cycle than more southern conspecifics.¹⁴

This paper examines how post-nuptial moult is modified in adult Willow Warblers, in relation to the breeding stage for birds breeding at latitude 54° 34'N in northeast England, and contributes information on the following questions. (1) Why do birds need to modify their moult? (2) How variable is the number of feathers renewed before moult is interrupted? (3) Do all late breeding Willow Warblers modify their moult?

MATERIAL AND METHODS

During mid-June to August (which covers the population moult period) 1988–96, 21–24

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ringing sessions were carried out each season at Lovell Hill Ponds, Wilton, Cleveland. All adult Willow Warblers were carefully examined for the presence of active moult on all primary and secondary feathers (numbered descendantly and ascendantly, respectively). No cases of an interrupted moult were recorded for male birds, therefore only females were included in this analysis. Females were sexed on cloaca, brood patch and/or wing-length.^{21–24}

Of 20 birds assumed to have suspended primary moult, eight had a known breeding history. A further 35 birds, which had neither started nor suspended post-nuptial moult when first caught, had a known breeding history (data collected 1982–96). First-egg dates for these and the eight in suspended moult were used to compare the two categories. In only six birds were first-egg dates known with any accuracy (nests found at egg stage). For the remaining birds, first-egg dates were back-calculated in time from age of young when ringed,^{4,5,24} assuming a 14-day incubation period and one day for the laying of each egg. To reduce any errors associated with this, first-egg dates were grouped into two-week periods (see Table 3).

Of the 35 non-moulting birds, 14 had started a full moult on recapture (moult present in other feather tracts) and moult start times for these birds were compared to the age of young at the time of moult initiation. Four birds

showed moult scores under 10, the remainder scores between 15–35.¹⁷ Moult start times for these birds were again back-calculated in time using 0.9 and 1.2 moult score per day for July and August respectively.²⁷ It has been shown that the higher the moult score the less precise the estimated start date will be.^{25,26} However any associated errors from this source were reduced by grouping start dates into half-month periods.

Any renewed primary feathers on birds suspending moult were carefully checked for any basal sheaths to ensure feather growth was complete. No cases of an interrupted secondary moult near the end of the post-nuptial moult cycle were noted.

The mean increase in moult score for eight birds undertaking a normally timed (i.e. mid- to late June) post-nuptial moult, and ringed and recaptured during moult stages 1–15, was compared to that of three birds ringed and recaptured actively growing the inner two primaries before a moult suspension.

RESULTS

The annual percentages of birds which were assumed or appeared to have suspended moult ranged widely from 11% to 46% each year (1988–96) and, overall, 32% of birds showed a modified start to moult (Table 1).

A total of 20 birds, with a variable number of inner primaries fully grown (1–4), were

Table 1. The number of adult Willow Warblers caught each year showing a modified start to post-nuptial moult. On all birds no other feather tract was in active moult.

Year	Normal active moult	Suspended moult	Probable suspended moult	Possible suspended moult p1–2 full-grown, p3–4 growing
1988	11	2	3	–
1989	7	2	4	–
1990	13	2	1	–
1991	11	3	3	–
1992	9	1	2	–
1993	5	2	0	–
1994	8	4	2	–
1995	8	1	0	2
1996	6	3	2	3
Totals	78	20	17	5

–, Not noted.

Table 2. The number of inner primary feathers renewed before a moult suspension in 20 adult female Willow Warblers caught in July and August 1988–96.

Month	Number of feathers renewed				Mean no. of feathers
	1	2	3	4	
July	1	11	3	0	2.1
August	0	1	2	2	3.0

assumed to have suspended moult (Tables 1 & 2). Three of these birds had recommenced moult at the point of suspension (primaries 1 & 2 full-grown, primaries 3 & 4 in pin) when recaptured seven, nine and 11 days later. These were the only birds to be safely identified as undertaking a moult suspension.

Another 17 birds were caught with the inner two primaries well-grown (score 2–4).¹⁷ Two of these birds, when recaptured six and eight days later, had both feathers full-grown and had probably suspended moult (Table 1). A further five birds were caught in August 1995 and 1996 with the inner two primaries full-grown and primaries 3 and 4 at moult score 2 and 1, respectively. Similar cases in previous years

Table 3. First-egg dates for 21 adult female Willow Warblers (all nestlings younger than 25 days) showing no active moult when first caught, 14 in active moult when recaptured (data collected 1982–96) and for eight birds in suspended moult 1988–96.

	First-egg dates					Totals
	May		June		July	
	1–14	15–31	1–14	15–30	1–15	
No active moult	2	6	10	2	1	21
Start of full moult						
16–30 June	2	0	0	0	0	2
1–15 July	1	4	1	0	0	6
16–31 July	0	0	3	2	1	6
Suspended moult	0	0	0	7	1	8
Total	5	10	14	11	3	43

were probably overlooked.

In all the above cases no other feather tract showed active moult. This is contrary to the usual sequence of a normal full post-nuptial moult, when body feathers and particularly all greater coverts commence moult before the first two primaries have reached growth stage 2.²⁷ The mean number of feathers renewed before a moult interruption was significantly higher for birds caught in August than in July ($t_7 = 2.89$, $P < 0.05$, Table 2). The majority of birds suspending moult showed first-egg dates of 16–22 June, compared to the earlier dates for the majority of birds not suspending moult ($\chi^2_1 = 4.7$, Yates' correction, $P < 0.001$, Table 3).

The moult start times for 14 adult female Willow Warblers which did not suspend moult are shown in Table 4 in relation to the mean age of their young. Although moult appeared to start at an earlier nestling stage in each half-month period, none of the differences was significant (ANOVA $F_{2,11} = 2.67$, ns).

The mean daily primary moult score rate for birds during early moult (scores 1–15) which undertook a normal-timed moult (i.e. end of June) was significantly higher than for birds which suspended moult, Table 5 ($t_9 = 2.89$, $P < 0.05$).

DISCUSSION

Suspension of a post-nuptial moult has been attributed to further breeding attempts taking place^{4,17,28} but proof has rarely been recorded.^{4,29} Not all late-breeding female Willow Warblers in this study showed a suspended moult. This could be due to the timing of replacement clutches. First-egg dates for the majority of

Table 4. Moult start times during June and July for 14 adult female Willow Warblers in relation to mean age of young 1982–96.

Moult start times	Mean age of young (days) \pm sd
16–30 June	27.5 \pm 2.1
<i>n</i>	2
01–15 July	22.6 \pm 4.2
<i>n</i>	6
16–31 July	20.0 \pm 4.0
<i>n</i>	6

Table 5. The mean increase (\pm sd) in moult score per day for female Willow Warblers suspending moult and not suspending moult, 1988–96.

	No. of birds	Mean no. of days between captures	Mean increase in moult score	Mean moult score per day
Suspended moult	3	8.3 \pm 2.1	4.0 \pm 0.0	0.5 \pm 0.1
Not suspending moult	8	6.4 \pm 1.8	5.6 \pm 1.1	0.9 \pm 0.2

birds suspending moult occurred during 16–22 June.

This period coincides with the earliest start of a full post-nuptial moult in birds (especially males) which have successfully reared a normally timed brood through to independence.⁴ If, as suggested previously, moult is timed endogenously,^{4,30,31} then females starting to lay during 16–22 June may have initiated moult but suppressed it,^{32–35} triggering a suspension or very slow rate of renewal until young had achieved independence.^{20,36}

Such a small window in which a moult suspension could occur may account for other late-breeding females which did not suspend moult. In these cases, another pattern seems to occur with females initiating their full post-nuptial moult at an earlier stage of the breeding cycle (i.e. before young attain independence), compared with those birds suspending moult of inner primaries (Table 4). It is possible that these birds were responding to environmental factors such as photoperiod, which would be much shorter for them than individuals which suspended moult in early July (see ref. 37 and references therein).

A similar picture for both male and female Willow Warblers during breeding occurs regularly in Finland,⁵ Sweden³⁸ and in north-west Russia.²⁰ In the latter locality, some birds started renewal of one to three primaries during incubation and either stopped before full growth was achieved or the rate slowed down during the most intensive part of the breeding cycle, i.e. the feeding and caring of young.²⁰

The number of inner primaries replaced prior to a moult suspension was significantly higher for birds caught in August than July (Table 2). This suggests in some birds the partial renewal process is not suspended but slowed down; only when the first few inner

primaries are full grown are adjacent ones dropped. This is supported by the five birds caught during August 1995 and 1996. They showed primaries 1 and 2 full grown and 3–4 at moult stages 2 and 1, respectively (Table 1).

However, the breeding stage of these females was not known. Either their young had reached independence (which is unlikely as no other feather tract was in active moult; see Methods), allowing adults to recommence their full moult, or birds were undertaking a protracted moult while still attending eggs or young.

To sum up. At my study site three patterns of moult initiation have been identified in female Willow Warblers attending late broods:

1 A suspension of moult after the renewal of the inner two primaries, which is recommenced at the point of suspension, shown definitely in only three birds.

2 A very slow rate of moult of up to four inner primaries with no moult initiation in other feather tracts. Moult probably proceeds into a full post-nuptial moult when breeding ceases.

3 The full moult takes place at an earlier stage of the breeding cycle, i.e. before young leave parental care, unlike normally timed moulting birds or those suspending moult.

With each of these modifications in the start of moult, the full moult would be completed at an earlier date than if all birds waited until young had achieved independence before the initiation of the full moult.

No Willow Warblers (male or female) have been caught at this site with an interrupted moult in the secondary feather tract at the end of the post-nuptial moult cycle. This is in contrast to Sweden and Russia where this occurs regularly.^{20,39} This difference probably reflects the more stringent time constraints for birds breeding at more northerly latitudes¹⁴ and is a further adaptation to allow migration to take place at the earliest opportunity.

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