Timing of the onset of postnuptial moult in the Willow Warbler *Phylloscopus trochilus* in relation to breeding in southern Finland

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The timing of the postnuptial moult was studied in the Willow Warbler, a long-distance migrant whose breeding grounds offer favourable conditions for a restricted period. Altogether 92 individuals were examined in southern Finland, including 21 males and 39 females whose exact stage in the breeding cycle was known.

Both sexes started moulting independently of the breeding stage, females probably about 10—15 days later than males. The moulting rate seems to be slower in early moulting individuals than in later ones, differing both within and between sexes. The earliest moulters may be those whose nests are destroyed.

In Finnish Willow Warblers adjustment to the short summer is achieved by a rapid rate of moulting and overlap between breeding and moulting.

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Introduction

The schedule of birds most commonly consists of non-overlapping breeding and moulting phases, especially in temperate and northern latitudes (Payne 1972). In high latitudes, the period during which conditions are favourable for birds is very short. When the favourable season is longer, birds may be able to moult fairly slowly after one, two, or even three clutches.

As the time between completion of the breeding cycle and the end of the favourable season becomes shorter, the following adjustment strategies are possible: (1) a rapid moult, (2) overlap between breeding and moulting, (3) overlap between moulting and autumnal sexual activity and territoriality, (4) overlap between moulting and migration, (5) migration with a suspended moult, or (6) postponement of the moult till after migration. The adjustment strategy may vary inter- and intraspecifically, and between and within populations (e.g. Evans 1966, Newton 1966, 1968, Stresemann & Stresemann 1966, Dolnik & Bluymenthal 1967, Haukioja 1971a, Dhondt 1973, Hyytiä & Vikberg 1973, Pimm 1973, Ginn 1975, Orell & Ojanen 1980, Kasparek 1980).

Proper timing of the onset and rate of the postnuptial moult may be of crucial importance for a bird living in a strongly seasonal environment, because overlap between the moult and the other above-mentioned activities, or an extremely rapid moult, may be

too stressful. This paper describes the early phases of the postnuptial moult of the Willow Warbler *Phylloscopus trochilus,* a long-distance migrant wintering in the tropics, and relates the observations to data on the breeding cycle in a south Finnish population. The Willow Warblers spend roughly three and a half months at their breeding grounds in southern Finland, from the second half of May to the end of August or beginning of September. Breeding commences soon after the arrival of the females, and the nestling stage lasts to the first, sometimes to the second, half of July, occasionally to early August (v. Haartman 1969, my own observations). The exact phase of the breeding cycle was known for many of the individuals examined for primary moult in the study population. The postnuptial moult of Finnish Willow Warblers has been described earlier by Haukioja & Kalinainen (1968), Haukioja (1971a, b), Niemelä (1974), and Lehikoinen & Niemelä (1977), but without any data on the breeding phase. The moult of Karelian and north Norwegian Willow Warblers has been briefly investigated by Dolnik & Bluymenthal (1967) and Evans (1971), respectively.

Material and methods

Numerous Willow Warblers have been ringed since 1972 during a study of the population ecology of the species at Lammi Biological Station (61°03'N, 25°03'E), southern Finland. Most of the adult birds trapped at nests or in mist-nets after mid-summer were checked for primary moult (36 males, two of them twice during the same season, 54 females, one of them in two consecutive years, and 2 unsexed individuals). The birds were sexed according to the behaviour during the breeding cycle, properties of the brood patch, form of the cloacal protuberance and/or (for 6 birds late in August) the wing length (see Tiainen 1981a). The exact stage of the breeding cycle was known for 21 males and 39 females, either from observations on egg laying, or hatching of the young, or from measurements of the wing lengths of their nestlings (Tiainen 1978).

Only the primary moult was studied. The stage of the moult was recorded by scoring each of the nine primaries as follows: 0 if old, 1 if missing or in pin, 2 or 3 if 1/3 or 2/3 of the final length, respectively, 4 if growth almost completed, and 5 if growth fully completed. These values were summed up for a primary score ranging from 0 to 45 (e.g. Newton 1966). All the birds were weighed with a 30-g Pesola spring balance with an accuracy of 0.1 g. As the main purpose of trapping was to mark breeding Willow Warblers for the population study, systematic capturing was usually discontinued after the breeding season. More or less irregular netting conducted later yielded only a few adult Willow Warblers.

Results

The moulting rate of the Willow Warbler varies considerably. The rate, or the daily increase of the primary score, was 0.76 points for a male examined twice when moulting (Fig. 1). The rate for another male examined twice cannot be calculated exactly, but exceeds 0.76. The rates calculated for two individuals captured repeatedly at intervals of over one week in Pori at the end of July and in the first half of August (see Fig. 1 in Haukioja & Kalinainen 1968) were c. 1.3—1.4 points/day. The average rate for Finnish Willow Warblers is about 1.1 points/day (Lehikoinen & Niemelä 1977). If the increase of the primary score is assumed to be linear (Newton 1967), the onset of the moult of an individual can be calculated from the recorded date and primary score, but the higher the score, the more uncertain is the result, because of the great variation in the rate. The above records suggest that the rate is slow in early moulting birds and faster in late moulters. Hence, a slower rate is applied below in calculating the starting days.

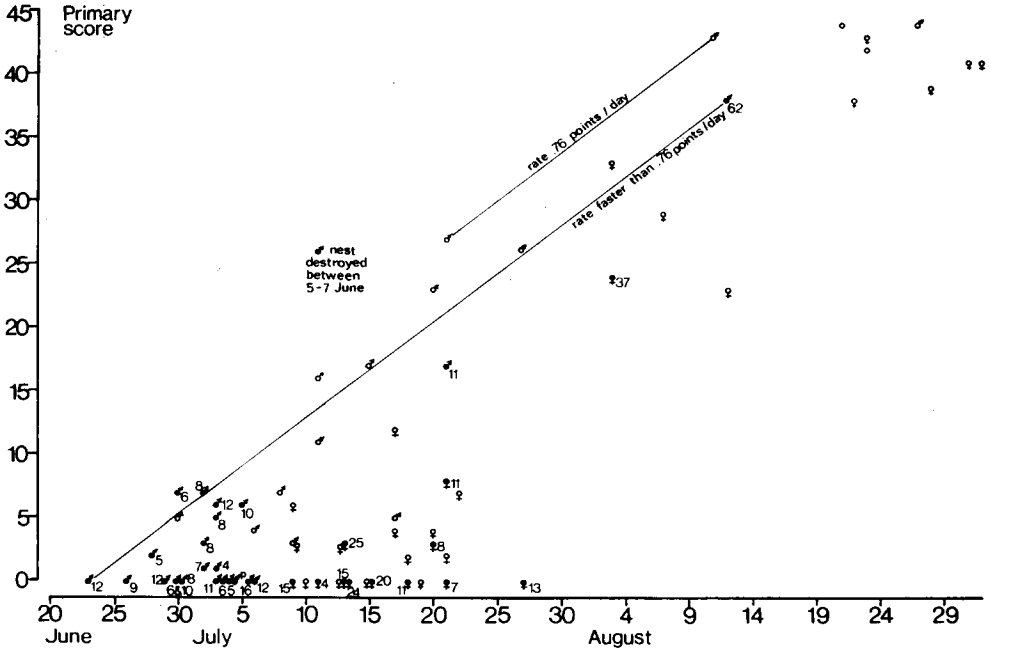

FIG. 1. Primary scores of Willow Warblers in Lammi in 1972—1980. Black signs represent birds whose breeding stage was known. Two birds were not sexed. The figures beside the symbols give the age of the nestlings on the date of the record (p = nestlings whose age was unknown). Straight lines connect successive records of the same birds in the same season. The following birds, which had not started moulting, were not marked in the figure: one female with eggs, eight females with 4—12-day-old nestlings and two females whose nesting stage was unknown examined on 1—7 July, and 12 females with 4—11-day-old nestlings examined on 23—30 June.

The first moulting male was captured on 28 June. It had a primary score of 2, and 5-day-old nestlings (Fig. 1). When the rate of 0.8 points/day was used to calculate the starting dates of the early moulting males, the earliest day obtained was 10 June. The nest of the bird in question had been destroyed a few days before that date. The onset dates calculated for 11 males whose nesting stage was known are given in Table 1. Here, a possible error in the choice of the moulting rate of 1.0 points/day does not greatly affect the results for the nine males with observed scores of 7 or less.

From Table 1 and Fig. 1 it appears that the stage of the nesting cycle does not affect the onset of the postnuptial moult in Willow Warbler males. The first males may begin moulting as early as the incubation phase or when the eggs are hatching (nos. 1 and 10 in Table 1; the hatching date was close to the population average in the first case, but one of the latest in the second). On the other hand, many males with 5—12-day-old nestlings, or even fledged 16-day-old young had not begun moulting at the beginning of July.

To check whether the physiological condition of the male affects the onset of the moult, the mean weights ± *SD* were calculated for non-moulting and

moulting males whose stage in the breeding cycle was known. Only weight records from 28 June — 6 July and males at the beginning of the moult (primary score 7 or less) were accepted, to avoid possible effects of weight variation due to the phase of the season and stage of the moult (cf. Lehikoinen & Niemelä 1977, Tiainen in prep.). The figures did not differ significantly (9.34 ± 0.621 g for 11 non-moulting, and 9.29 ± 0.405 g for 9 moulting males). Possible yearly differences cannot be studied from the available data.

The nesting stage was known for only four moulting females (Fig. 1 and Table 1). The last non-moulting female was trapped on 27 July, when her nestlings were 13 days old. Since the majority of the females examined had not started moulting, it is impossible to determine the exact difference in starting date between males and females, but it seems to be at least 10, perhaps some 15 days. The females start moulting at a later nesting stage than the males, but the stage does not seem to affect the onset date directly. At the four latest nests, two females were being assisted by the male in feeding the nestlings, but two were alone. Of the two unassisted females, that caught on 20 July had started moulting (primary score 3), whereas that caught on 27 July had not. Similarly, only one of the two assisted females had started moulting. Thus the presence or absence of the male does not seem to affect the onset of moulting in late nesting females.

It has already been suggested that moulting is more rapid in late than in early moulters. As females moult later than males they ought to moult more rapidly. The moulting rate may be increased either by growing more feathers simultaneously, or by increasing the growth rate of individual primaries. The first possibility was tested visually by plotting the number of simultaneously growing primaries against the primary score in Fig. 2 (the data are too restricted for statistical tests as both the date and the stage of the moult ought to be considered). Fig. 2 indicates that the onset of the moult in males may be more abrupt in late than in early starters. A striking example of an abrupt start is provided by the male captured on 17 July with simultaneously shed primaries. Fig. 2 also slightly supports the idea that the females moult faster than the males.

TABLE 1. Dates of onset of postnuptial moult in Willow Warblers whose nesting stage was known calculated by assuming that the primary score increased at a rate of 1.0 points/day. Age of nestlings given in days before (sign -) or after hatching. Nos. 1—11 are males, 12—15 females.

Bird no.	Date of onset	Age of nestlings	Observed score and date
1	24 June	0	7/30 June
2	26 June	2	7/ 2 July
3	27 June	4	3/28 June
4	28 June	7	6/ 3 July
5	29 June	4	5/ 3 July
6	30 June	5	6/ 5 July
7	30 June	6	3/ 2 July
8	2 July	7	1/ 2 July
9	3 July	4	1/ 3 July
10	5 July	-5	17/21 July
11	6 July	25	38/12 August
12	11 July	14	24/ 3 August
13	11 July	23	3/13 July
14	14 July	4	8/21 July
15	18 July	6	3/20 July

Discussion

For a bird, territoriality, breeding, moulting, migration and sometimes perhaps also preparation for the winter increase the energetic demands (Payne 1972, King 1974, Berthold 1975, Ken-

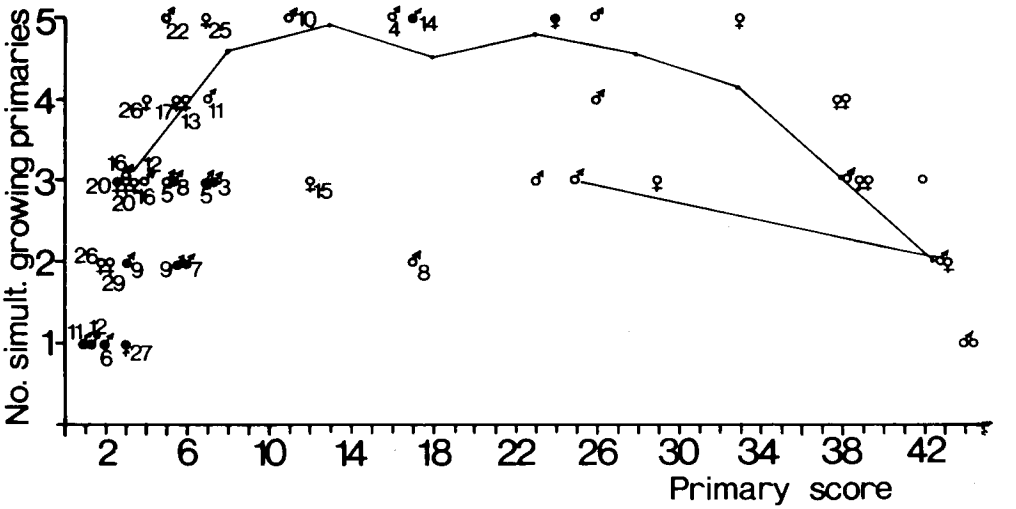

FIG. 2. The rate of the primary moult in the course of the moulting cycle. Black signs: birds with nestlings, sign with oblique stroke: bird with fledglings, open signs: birds whose nesting stage was unknown. The figures indicate the dates calculated for the onset of the moult (nil on 20 June; primary score assumed to increase linearly by 1.0 points/day). The curve shows the average number of simultaneously growing primaries in various stages of the moulting cycle of Finnish Willow Warblers (N = 634, Lehikoinen & Niemelä, pers. comm.; from Lehikoinen & Niemelä 1977). The straight line connects two records from a single individual.

deigh et al. 1977). Thus, the physiological strain encountered would be lowest if the different phases of the annual cycle could be completed without overlap and at a moderate rate. But overlaps and a faster rate may be adaptive in a seasonal environment with a short favourable period. When increased beyond certain limits, however, the overlap and rapid moulting rate will become too strenuous. Moreover, overlap of moulting with phases when full efficiency of flight is necessary will also be maladaptive.

In the Willow Warbler, the moult is one of the shortest among Finnish birds, lasting only c. 40 days in both southern Finland and Lapland (Lehikoinen & Niemelä 1977, cf. also Evans 1971). It is possible that the moulting rate of the Willow Warbler is already maximal, and that the strategy chosen for further adjustment to the still existing shortage of time has been overlap between breeding and moulting.

Other long-distance migrants breeding in the North have chosen postponement of moulting till after migration (e.g. *Phylloscopus sibilatrix* and *Sylvia borin,* Stresemann & Stresemann 1966), slight overlap of moulting and migration (e.g. *Ficedula hypoleuca,* Hyytiä & Vikberg 1973), or migration with suspended moult (e.g. *Muscicapa striata* and *Sylvia communis,* and some others, Hyytiä & Vikberg 1973, Pimm 1973, Mead & Watmough 1976). On the other hand, breeding and moulting may also overlap slightly in *Ficedula hypoleuca* in our study area (Solonen & Tiainen, unpubl.). Such overlap can be expected to occur in many other northern long-distance migrants, too. In the northernmost Willow Warbler populations, the possibility of a slight overlap between moulting and migra-

tion cannot be excluded, either, although Willow Warblers in primary moult have not been caught at Finnish bird stations in the Åland archipelago (Vikberg 1974). Willow Warblers caught at central European ringing stations during migration time often have moulted body feathers (Berthold, pers. comm.), and 3.2 % (6 out of 250) of the Willow Warblers caught in Iberia migrated with suspended moult of secondaries but not of primaries (Mead & Watmough 1976).

A slow rate of moulting might be advantageous for the Willow Warbler, since this is not so strenuous physiologically and guarantees better flight ability throughout the moult (Haukioja 1971b). Individuals which have a longer period at their disposal (the earliest ones) evidently tend to moult most slowly (Figs. 1 and 2). Extrapolation of the slowest observed rate, 0.76 points/day, for the whole moulting period would give a duration of 59 days, or 50 % more than the average of all Finnish Willow Warblers (calculated by the regression method, Lehikoinen & Niemelä 1977). The average ($\pm$ *SD*) duration of the postnuptial moult of 5 captives held in natural conditions in SW Germany was 50.2 days $\pm$ 8.1, but only 42.0 days for three other captives held in a constant light: dark cycle of 12:12 h, which resembles the natural conditions in northern latitudes in autumn, after the normal moulting period (Gwinner 1973). These observations also support the idea that the northern Willow Warbler populations encountering the shortest favourable seasons may have the shortest possible postnuptial moult. In many species with a prolonged moult, the northern populations moult faster than the southern ones (Orell & Ojanen 1980 and references therein).

Gwinner (e.g. 1968, 1972) showed that the schedule of the annual cycle is controlled endogenously in the Willow Warbler. In captive Willow Warblers held for several years in constant conditions, the timing of moults, migratory disposition and migratory restlessness lies on a free-running circannual basis with a shorter annual cycle than a calendar year. In nature, the endogenous cycle is synchronised with the calendar year by the annual photoperiodic cycle.

The present study shows that the onset of moulting has no fixed connection with the end of nesting. Nor does it depend on any distinct critical daylength. It is not possible at present to determine what controls the fine tuning of the onset of the postnuptial moult in individual Willow Warblers, but an endogenous rhythm offers one possible explanation. Free-running circannual rhythms with a shorter cycle than the calendar year may allow a bird to enter the next phase of the cycle earlier than normal if the conditions are changed (Berthold 1974). This could explain the exceptionally early starting date in one bird in this study, and perhaps also other early cases (cf. Payne 1972, Silverin 1979: possible inhibitory role of reproductive hormones).

The onset of moulting is significantly earlier in Willow Warbler males than females, which has also been observed in many other species (Orell & Ojanen 1980 and references there). The data in Fig. 1 and the average moulting season of south Finnish Willow Warblers, 5 July — 25 August (Lehikoinen & Niemelä 1977), suggest that the intersexual difference is smaller in the termination than the onset dates, which agrees with the observation that females may tend to moult rapidly (Fig. 2; cf. Dhondt 1973, Orell & Ojanen 1980). In spite of the differ-

ence in the rate, the moult is completed earlier in males, which may have adaptive value in preventing overlap with the autumnal territorial phase, and conferring readiness for combat with juvenile males. The lower moulting rate in males than in females may be simply the result of the earlier onset. The adaptive value of the later onset in females must lie in its promoting the parental care of the nestlings and fledglings. Although the males shared feeding duties at all but two of the late nests studied, they may regularly decrease their attendance towards the end of the nesting phase (Steinfatt 1939, Kuusisto 1941, Tiainen 1981b), and perhaps give it up completely during the fledgling stage (Silverin 1979).

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Selostus: Pajulinnun postnuptiaalisen sulkasadon alkamisen ajoittuminen suhteessa pesintään

Pajulinnun postnuptiaalisen (pesinnän jälkeisen) sulkasadon ajoittumista tutkittiin Lammin biologisen aseman alueella populaatiotutkimuksen yhteydessä kerätyn aineiston perusteella. Tutkittuja yksilöitä oli kaikkiaan 92, joista 21 koiraan ja 39 naaraan tarkka pesinnän vaihe oli tiedossa. Molemmat sukupuolet aloittivat sulkimisen pesinnän vaiheesta riippumattomasti, naaraat n. 10—15 päivää koiraita myöhemmin (kuva 1, jossa y-akselilla ovat käsisulkien sulkimisluvut ja x-akselilla vastaavat päivämäärät, mustattujen merkkien rinnalla olevat luvut ilmaisevat poikasten iän kyseisenä päivänä; taulukko 1). Varhaisimmat sulkijat olivat mahdollisesti pesänsä menettäneitä; kaikkein varhaisimman koiraan pesän tuhoutuminen olikin tiedossa. Sulkimisnopeus näyttää olevan hitaampi varhaisilla kuin myöhäisillä koirailla ja koirailla hitaampi kuin naarailla. Koiraat ehtinevät tästä huolimatta lopettaa sulkasatonsa ennen naaraita, millä voi olla merkitystä syksyisen sukupuolisen aktiivisuuden aikana, jolloin vanhat koiraat joutunevat puolustamaan asemaansa pesimäpaikoillaan nuoria koiraita vastaan. Naaraiden myöhemmin alkava sulkasato varmistaa poikasille paremman huolenpidon kuin jos molemmat emot alkaisivat samanaikaisesti varhain sulkasatonsa.

Pohjoisen linnuilla on valittavanaan useita eri mahdollisuuksia lyhyestä kesäkaudesta aiheutuvan aikapulan ratkaisemiseksi. Tutkitun populaation pajulinnut ratkaisevat oman aikatauluongelmansa pesimällä vain kerran, sulkimalla äärimmäisen nopeasti ja aloittamalla sulkimisen osittain hieman ennen pesintävaiheen loppumista. On odotettavissa että sulkasadon tutkiminen pesinnän loppuvaiheissa paljastaisi pesinnän ja sulkimisen päällekkäisyyttä monissa pitkän matkan hyönteissyöjämuuttajien pohjoisissa populaatioissa, sikäli kuin sulkiminen tapahtuu pesimäalueilla.

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