

Interrupted moult of adult Willow Warblers *Phylloscopus trochilus* during autumn migration through Sweden

ANDERS HEDENSTRÖM, ÅKE LINDSTRÖM & JAN PETTERSSON

Abstract

Among passerines a complete moult is carried out annually after breeding in the summer season or, in some long-distance migrants, after autumn migration in the winter season. A few species, such as the Willow Warbler *Phylloscopus trochilus*, show two complete annual moults. It is often observed that among Willow Warblers on autumn migration passage a few individuals retain one or more old secondaries, hence the moult after breeding has been interrupted. We hypothesise that the frequency of birds showing moult interruption should increase with increasing breeding latitude due to the shorter time available for breeding and moult towards north. Further, we expected a higher incidence of moult interruption in females compared with males because females presumably are more involved in breeding activities. These hypotheses were explored with data on adult Willow Warblers collect-

ed at Swedish bird observatories during a nation-wide co-operation project concerning the migration of the Willow Warbler. We found a positive correlation between the proportion of Willow Warblers with unmoulted secondaries and latitude. The proportion of females with moult interruption was higher than in males, and among birds with remaining old secondaries females had more unmoulted feathers than males. We found a rather high proportion of birds with interrupted moult at southern observatories, which we speculate may be associated with birds laying second clutches in some years.

*Anders Hedenström and Åke Lindström, Department of Ecology, Ecology Building, S-223 62 Lund, Sweden
Jan Pettersson, Ottenby Bird Observatory, Pl. 1500, S-380 65 Degerhamn, Sweden*

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Introduction

Most passerine birds undergo a complete moult once a year, normally just after the breeding season while still being in the breeding area, but in some species it is postponed until the birds have reached the winter quarters (e.g. Jenni & Winkler 1994, Kjellén 1994, Holmgren & Hedenström 1995). Among the species belonging to the Palaearctic-African migration system there is one unique species with respect to having two annual complete moults, namely the Willow Warbler *Phylloscopus trochilus* (Salomonson 1945, Underhill et al. 1992). However, it has recurrently been questioned whether the Willow Warbler really carries through two complete moults annually (e.g. Murton & Westwood 1977) and admittedly information is lacking about the moult for the most northern and eastern populations (Underhill et al. 1992). The northern populations presumably have less time to complete breeding and moult due to the short summers at northern latitudes.

Consequently, we may assume that pairs laying replacement clutches after having lost the first clutch will either be forced to moult faster than usual or to stop the moult at a certain stage and start the southward migration. Such birds will retain old and worn feathers during autumn migration. In this paper we report on the frequency and extent of such cases in adult Willow Warblers examined at Swedish bird observatories during autumn migration.

There are two principally different types of moult interruption. In *suspended* moult, the moult is subsequently resumed from the point at which it was stopped, while in *arrested* moult it subsequently starts at the normal site of initiation rather than at the point of interruption (Harper 1984). During passage migration it is unclear whether the birds have suspended or arrested moult, and we will therefore simply refer to interrupted moult.

In Sweden two subspecies of the Willow Warbler

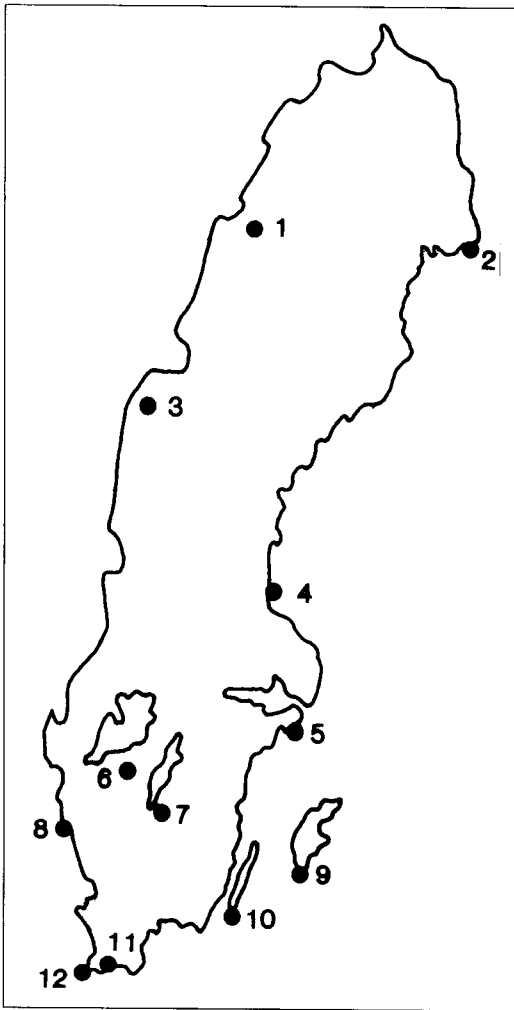


Fig. 1. Bird observatories and trapping sites where data on adult moult in Willow Warblers during autumn migration were collected. 1. Ammarnäs, 2. Haparanda Sandskär, 3. Ånnsjön, 4. Eggegrund, 5. Landsort, 6. Hornborgasjön, 7. Landsjön, 8. Nidingen, 9. Sundre, 10. Ottenby, 11. Jordberga, 12. Falsterbo. Geographical coordinates can be found in Table 1.

Fågelstationer och fångstplatser som samlat in data om adulta lövsångares ruggning under höstflyttningen samlats in. 1. Ammarnäs, 2. Haparanda Sandskär, 3. Ånnsjön, 4. Eggegrund, 5. Landsort, 6. Hornborgasjön, 7. Landsjön, 8. Nidingen, 9. Sundre, 10. Ottenby, 11. Jordberga, 12. Falsterbo. Platsernas koordinater återfinns i Tabell 1.

occur. In southern Sweden, up to about 60–63°N the nominate *P. t. trochilus* breeds. In northern Sweden it is replaced by *P. t. acredula* (e.g. Cramp 1992). The precise boundary between the two subspecies is

somewhat unclear. However, the southern subspecies migrates south-west during autumn towards wintering areas in West Africa, while the northern subspecies migrates south or south-east towards wintering areas in East and South Africa (Hedenström & Pettersson 1987).

Our hypothesis was that the frequency of unmoulted flight feathers should increase with increasing breeding latitude. Hence, we expected to observe more Willow Warblers with unmoulted flight feathers at northern observatories and at those stations mainly along the Swedish east coast, where the northern populations pass towards south-east (cf. Hedenström & Pettersson 1987). Furthermore, since breeding is likely to impose greater stress in terms of time and energy on the female (cf. Tiainen 1981), we expected to find a higher incidence of interrupted moult among females compared to males.

Methods

The data presented in this paper were collected in a co-operation project among Swedish bird observatories focusing on Willow Warbler migration (see Hedenström *et al.* 1989). Of special importance for the present analysis is that ringers were asked to carefully look for old, unmoulted flight feathers when examining adult birds. Special attention was given to the secondaries, which are the last feathers to be moulted in the normal moult sequence, and therefore in cases of interrupted moult, secondaries are the most likely feathers to be retained unmoulted. The data were collected during the years 1988–1990. During migration birds usually do not moult actively and the presence of old secondaries represent moult interruption. However, at Ammarnäs and Ånnsjön (see Fig. 1) Willow Warblers both breed and moult and it is not easily decided whether a bird shows interrupted secondary moult or simply did not finish moult yet. This can only be decided at the end of the primary moult; we therefore only included birds with a primary moult score of at least 40 points when secondary moult is completed or interrupted (see Ginn & Melville 1983 for moult scoring). Sex was determined on the basis of wing length (Fonstad & Hogstad 1981). To be on the safe side across the latitudinal span in this study we assigned birds of wing length of 69 mm or more to males and 66 mm or less to females (Hedenström & Pettersson 1984).

For passage birds at coastal bird observatories the relevant breeding latitudes to be used in statistical comparisons were unknown. Therefore, we simply used the latitude of the trapping site as representative

Table 1. Proportions of adult Willow Warblers with unmoulted (old) secondaries and the number of retained secondaries in those birds with at least one unmoulted secondary. Numbers within parentheses denote sample sizes. *Proportioner adulta lövsångare med oruggade armpennor och antalet oruggade pennor hos fåglar med minst en oruggad penna. Siffror inom parentes anger antalet undersökta fåglar.*

Locality <i>Plats</i>	Percentage	Percentage	Percentage	No. old	No. old	No. old
	Males (n)	Females (n)	All birds (n)	feathers Males (n)	feathers Females (n)	feathers All birds (n)
	<i>Procent hanar (n)</i>	<i>Procent honor (n)</i>	<i>Procent alla fåglar (n)</i>	<i>Antal oruggade armpennor hanar (n)</i>	<i>Antal oruggade armpennor honor (n)</i>	<i>Antal oruggade armpennor alla fåglar (n)</i>
Ammarnäs 65.58 N 16.05 E	16 (19)	50 (10)	28 (29)	2.7 (3)	3.5 (5)	3.1 (8)
Haparanda Sandskär 65.34 N 23.46 E	73 (11)	61 (33)	64 (44)	2.4 (8)	2.2 (20)	2.3 (28)
Ånnsjön 63.16 N 12.28 E	47 (17)	50 (30)	44 (110)	2.1 (8)	3.8 (15)	3.0 (49)
Eggegrund 60.42 N 17.11 E	36 (64)	49 (63)	42 (127)	2.1(23)	2.5 (31)	2.3 (54)
Landsort 58.46 N 17.52 E	8 (12)	0 (10)	4 (22)	3.0 (1)	– (0)	3.0 (1)
Hornborgasjön 58.19 N 13.34 E	43 (7)	33 (3)	40 (10)	2.0 (3)	3.0 (1)	2.2 (4)
Landsjön 57.52 N 14.21 E	0 (3)	0 (1)	0 (4)	– (0)	– (0)	– (0)
Nidingen 57.18 N 11.54 E	23 (86)	49 (76)	35 (162)	2.2 (20)	3.0 (37)	2.7 (57)
Sundre 56.53 N 18.11 E	10 (57)	40 (73)	27 (130)	2.7 (6)	2.7 (29)	2.7 (35)
Ottenby 56.12 N 16.24 E	23 (35)	29 (41)	26 (76)	2.6 (8)	2.8 (12)	2.7 (20)
Jordberga 55.26 N 13.25 E	17 (6)	0 (4)	10 (10)	5.0 (1)	– (0)	5.0 (1)
Falsterbo 55.23 N 12.49 E	16 (116)	47 (98)	30 (214)	2.2 (18)	2.9 (46)	2.7 (64)
Total <i>Totalt</i>	23 (433)	44 (442)	34 (938)	2.3 (99)	2.8 (196)	2.7 (321)

for the breeding origin of the birds examined. This certainly underestimates the true breeding latitude but the error should be similar across all localities.

We obtained complete data on secondary moult for all three of the project seasons from five sites, while two seasons were reported from five sites and one season from two sites. Hence, 12 sites contributed with data on adult moult (Fig. 1). However, in statistical calculations we only included data from sites where 10 or more birds were examined.

Results

On average 34% of the adult Willow Warblers had retained one or more old secondaries while on autumn migration (Table 1). The incidence of such unmoulted feathers varied geographically with a highest recorded value of 73% in males at Haparanda Sandskär. Across all sites (Landsjön excluded because only 4 birds were examined) there was a positive correlation between the proportion of birds with unmoulted secondaries and latitude ($r=0.56$, $df=9$, $P<0.05$). For the sexes separated this correla-

tion was $r=0.58$ ($df=9$, $P<0.05$) for males and $r=0.54$ ($df=9$, $P<0.05$) for females. Excluding also data from Landsort and Jordberga from the analyses due to few birds examined at these sites still result in positive correlation coefficients, but they are not statistically significant (both sexes: $r=0.51$, males: $r=0.61$, females: $r=0.43$; $df=7$, $P>0.05$).

Contrary to the prediction of a higher incidence of birds with interrupted moult at east coastal sites (Eggegrund, Landsort, Sundre, Ottenby) compared to west coastal sites (Nidingen, Falsterbo), 31% and 32% of the birds had moult interruption, respectively ($\chi^2=0.07$, $P>0.05$).

The number of unmoulted secondaries of those individuals having unmoulted secondaries showed no significant correlation with latitude ($r=-0.28$, $df=9$, $P>0.05$). There was a higher proportion of birds with unmoulted secondaries among females (44%, Table 1) than among males (23%, Table 1). We compared the number of cases (one case is the sample from one site in one year) where the proportion of females showing unmoulted secondaries was higher than for males, and found this in 14 out of 19

cases ($P=0.032$, Binomial test). We excluded sites where less than 10 birds were examined. The average number of retained old secondaries in birds with at least one unmoulted secondary was 2.3 for males and 2.8 for females (Table 1). Again we analysed the number of cases where the number of unmoulted secondaries was higher in females than in males, and found this in 12 out of 15 cases ($P=0.018$, Binomial test). Hence, a higher proportion of females than males had secondaries unmoulted in autumn and of those birds with unmoulted secondaries, females had a larger number unmoulted feathers than males.

Discussion

The data collected within this nation-wide project on Willow Warbler migration show that on average as much as one third of adult Willow Warblers retain on average 2.7 old secondaries when migrating southwards in the autumn. The proportion of birds with interrupted moult within the secondary feather tract increased from south to north. When comparing the sexes it emerged that a higher proportion of the females had secondary moult interruption. The females also had a higher number of unmoulted secondaries than the males.

Several studies have shown that in passerine species, normally having a complete flight feather moult in the breeding area (between breeding and autumn migration), some individuals may start migration without finishing moult (e.g. Hyytiä & Vikberg 1973, Mead & Watmough 1976, Swann & Baillie 1979). The pattern of increasing incidence of moult interruption with increasing latitude found in this study is in agreement with previous observations. Mead & Watmough (1976) studied the extent of interrupted moult of passage Willow Warblers of the subspecies *P. t. trochilus* in Spain. These birds probably originated in Western Europe. Mead & Watmough found 2.4% (out of 250 adult birds examined) of the Willow Warblers with old unmoulted secondaries. A similar study on Crete, with birds probably belonging to the subspecies *P. t. acredula* of northern and eastern Europe, showed that 9% (450 birds examined) of the Willow Warblers had unmoulted secondaries (Swann & Baillie 1979). The average number of unmoulted secondaries per bird examined on Crete was 3.0 (Swann & Baillie 1979). This is comparable to our result, but the proportion of individuals with moult suspension was higher in Sweden (*cf.* table 1). However, on Crete the proportion of birds with interrupted moult

was calculated on the basis of unaged birds. Hence, the true proportion adult Willow Warblers with interrupted moult should be substantially higher than 9% as reported and probably comparable to what we found in Sweden.

Among passage migrants in southern Sweden, we expected more birds of northern origin to be encountered at the stations on the eastern coast (e.g. Landsort, Sundre, Ottenby) than at the stations on the western coast (e.g. Nidingen, Falsterbo). An associated difference in the incidence of interrupted moult was not apparent in the data (Table 1). The reason for this is not clear, but one possible explanation to a rather high incidence of interrupted moult in southerly breeding populations could be that these birds may attempt replacement clutches or even a second clutch to a larger extent than further north. In such cases also relatively southerly populations of the Willow Warbler could end up in a time-conflict between moult completion and migration. However, this hypothesis remains to be tested by collecting data on breeding biology of Willow Warbler populations in southern Scandinavia.

What determines the decision to leave the breeding area without having finished moult? In a few species the birds keep all or most old secondaries until they reach the wintering area in the tropics. This seasonally divided or "split-moult" pattern has been well documented in the Barred Warbler *Sylvia nisoria* (Hasselquist *et al.* 1988, Lindström *et al.* 1993a), and seems to be a deliberately chosen strategy (Hedenström *et al.* 1992). However, the pattern found in the Willow Warbler rather indicates a flexible termination of the summer moult as a response to the environment. The time available for moult and fat accumulation after breeding and before autumn migration probably decreases with increasing latitude. Since both these processes require a substantial amount of energy (Lindström *et al.* 1993b), they have to be traded off against each other in situations of time stress or energy shortage (Lindström *et al.* 1994). The available insect food probably decline with progressing season (e.g. Haukioja & Koponen 1975). Hence, since a successful migration is primarily dependent on sufficient fuel reserves, the best alternative to cope with a stressful situation is probably to adjust the moult. There are indications that the speed of moult at northern latitudes cannot be increased any further (Lindström *et al.* 1994). Hence, the remaining option is to moult as far as possible and then interrupt the moult at some stage which still allows fat accumulation for a successful departure. It is not known if individuals with moult interruption

resume moult after migration and renew those feathers which were skipped during the main moult period (Jenni & Winkler 1994). The fitness cost of leaving a few secondaries is probably not dramatic for Willow Warblers as they will undertake a complete moult in the wintering quarters anyway (Underhill *et al.* 1992).

The stress hypothesis is further supported by the fact that females, which are more involved in the breeding activities (Tiainen 1981), showed a higher incidence of interrupted moult than did males. Onset of moult in female Willow Warblers shows a correlation with brood size (Bensch *et al.* 1985), indicating that females rearing many young may pay for this in terms of an interrupted moult.

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Sammanfattning

Avbruten ruggning hos adulta lövsångare under höstflyttningen genom Sverige

Normalt genomför tättingar en fullständig ruggning varje år. Ruggningen sker normalt antingen direkt efter slutförd häckning medan fåglarna fortfarande befinner sig i häckningsområdet, eller så sker den efter höstflyttningen i vinterkvarteren. Det finns några undantag från dessa mönster, däribland lövsångaren *Phylloscopus trochilus* som årligen genomför två kompletta ruggningar under sommar respektive vinter. Man har tidigare observerat att en del lövsångare ger sig iväg på höstflyttning med en eller några gamla och oruggade armpennor, något som brukar benämnas avbruten ruggning. Det är rimligt att förmoda att avbruten ruggning beror på att fågeln hamnat i tidsnöd mellan å ena sidan att slutföra ruggningen och å andra sidan att komma iväg i tid på flyttningen söderut. På grund av att sommarsången blir kortare ju längre norrut man förflyttar sig, bör fåglar som häckar i norr vara mer tidspressade än i söder och vi förväntar oss därför en ökande andel fåglar med avbruten ruggning längs en syd-/nordlig gradient. Förmodligen är honan mer engagerad i häckningsbestyren än hanen. Om så är fallet förväntar vi oss även en större proportion fåglar med avbruten ruggning bland honor än bland

hanar. Hos fåglar som uppvisar avbruten ruggning förväntar vi oss ett större antal oruggade armpennor hos nordliga jämfört med sydliga populationer och inom samma population förväntar vi oss att honor uppvisar större antal oruggade pennor än hanar.

Vi testade dessa hypoteser utifrån ett material på höstflyttande lövsångare som examinerades på svenska fågelstationer och fångstplatser. I genomsnitt uppvisade 34% av adulta lövsångare avbruten ruggning (Tabell 1). Vi fann en positiv korrelation mellan proportionen fåglar med avbruten ruggning och latitud ($r=0,56$, $df=9$, $P<0,05$). Däremot fann vi inget statistiskt signifikant samband mellan antalet oruggade armpennor hos fåglar med avbruten ruggning och latitud ($r=-0,28$, $df=9$, $P>0,05$).

Andelen honor som uppvisade avbruten ruggning (44%, Tabell 1) var högre än andelen hanar med avbruten ruggning (23%, Tabell 1). Antalet oruggade armpennor bland fåglar med avbruten ruggning var högre hos honor (2,8) än hos hanar (2,3).

Sammanfattningsvis fann vi resultat rörande proportionen lövsångare med avbruten ruggning i stort sett i linje med våra prediktioner. Undantaget utgjordes av antalet oruggade pennor hos fåglar med avbruten ruggning i relation till latitud. Det verkar alltså som om nordligt häckande populationer är mer tidspressade än sydligt häckande populationer och har svårare att hinna med att både häcka och att slutföra ruggningen före höstflyttningen.