The Seasonally Divided Flight Feather Moult in the Barred Warbler Sylvia nisoria: A New Moult Pattern for European Passerines

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Wing and tail feather moult in Barred Warblers was studied during three summers in SE Sweden. Birds arriving at their breeding grounds had on average 3.2–4.9 fresh secondaries and 3.9–9.4 fresh tail feathers, most certainly moulted in winter quarters. A few primaries and tertials had also been renewed. After breeding, normally all primaries and tertials were moulted. Primary moult duration was approximately 40 d for the individual and 60 d for the population. On average, only 0.7–1.4 secondaries were shed. No individuals renewed any winter-grown secondaries the following summer. Normally, 3–4 (mainly central) tail feathers were moulted. Thus, Barred Warblers moult primaries, tertials and central tail feathers in summer, and secondaries and a varying number of tertials and tail feathers in winter. The juvenile winter moult of secondaries shows that the seasonally divided flight feather moult is actively initiated already in the first winter; this is interpreted as a preparation for an early departure from breeding grounds the following summer. This moult pattern has not previously been documented in European passerines.

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Introduction

In most European passerines, adult birds moult completely immediately after breeding, i.e. they renew all flight and body feathers. Juveniles either moult completely (e.g. larks Alaudidae) or just renew a variable amount of their body feathers and wing coverts (e.g. thrushes Turdidae), and sometimes also tertials and tail feathers (e.g. tits Paridae). This pattern is typical for birds wintering in temperate regions where both age classes undergo no or only a partial moult in winter. However, this pattern is also found in some species wintering in tropical regions (e.g. some wagtails and pipits Motacillidae, the Nightingales *Luscinia* spp and the Redstart *Phoenicurus phoenicurus*). A possible variant of this moult pattern is the interrupted moult, a rather poorly understood strategy where adults of mainly tropically wintering species leave some secondaries unmoulted before autumn migration (see e.g. Hyytiä and Vikberg 1973, Mead and Watmough 1976, Swann and Baillie 1979). Aidley and Wilkinson (1987) showed that some Whitethroats *Sylvia communis* moult a few secondaries in winter which indicates a resumption of the interrupted moult.

A second main moult pattern is characterized by both age groups moulting only partially just after breeding and then moulting completely in the winter quarters. This pattern is found only in birds wintering in tropical regions (e.g. warblers of the genera *Acrocephalus, Hippolais* and *Locustella*). Information on moult in European passerines can be found in e.g. Stresemann and Stresemann (1966), Ginn and Melville (1983), Busse (1984) and Svensson (1984).

Detailed studies on passerine moult have reported

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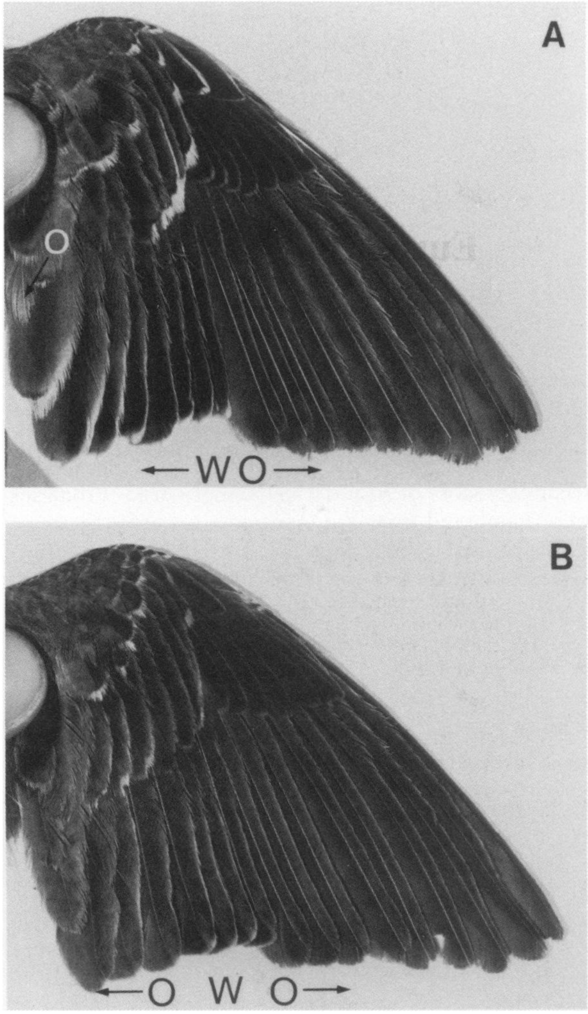

Fig. 1. The occurrence of winter moulted wing feathers as shown by two Barred Warblers caught in summer at Ottenby, SE Sweden. W = winter shed feathers, O = feathers not moulted in winter.
(A, top): 3y+ male examined 3 July 1987. This individual had moulted all secondaries as well as the two outer tertials in winter. These W feathers have broad white tips and are noticably fresher than the O feathers.
(B, bottom): 4y female (ringed in 1985 as 2y) examined 4 July 1987. The four outermost secondaries have been moulted in winter. They have some white on their tips and are slightly shorter and less worn than the O feathers. (Photos: Karin Persson.)

several divergent moult patterns, e.g. in the River Warbler *Locustella fluviatilis* (Pearson and Backhurst 1983), the Savi's Warbler *L. luscinioides* (Thomas 1977), the Willow Warbler *Phylloscopus trochilus* (Salomonsen 1945) and the Spotted Flycatcher *Muscicapa striata* (Stresemann and Stresemann 1966). As more detailed data on moult are gathered it becomes obvious that species, subspecies, and individuals show a great deal of plasticity in their moult patterns, most certainly as an adaptation to different ecological conditions.

In the genus *Sylvia*, 14 out of 16 Palaearctic species have been presumed to have a complete summer moult; in the remaining two cases, the Garden Warbler *Sylvia borin* and the Whitethroat (Asian races *S. communis icterops* and *volgensis*), the prevalent moult pattern is a complete winter moult (Williamson 1968, Stresemann and Stresemann 1968). However, irregularities are frequently observed in most *Sylvia* species and for some species data on moult are still scanty, e.g. the Barred Warbler *S. nisoria*.

The Barred Warbler breeds from the Baltic and France eastwards to Mongolia (Moreau 1972, Harrison 1982). In Sweden it is a scarce breeder mainly in the southeastern part of the country (SOF 1978). It winters in N and E Kenya, NE Tanzania and Ethiopia; rarely elsewhere (Moreau 1972, Pearson 1978, pers. comm.). Its moult has been presumed to follow the first major moult pattern outlined above (Witherby et al. 1943, Williamson 1968, Schmidt 1981, Busse 1984, Svensson 1984). However, beside the moult of body-feathers, several authors report a winter moult including a varying number of secondaries, tertials and tail-feathers (Witherby et al. 1943, Williamson 1968, Schmidt 1981). Pearson (1978) adds that some first year birds moult their outer primaries in winter. Without giving any detailed data, Fracasso (1985) gives a general description of the year-round moult pattern of the Barred Warbler: primaries, tertials and some secondaries are moulted in summer and some secondaries are moulted the following winter. However, no systematic study on the moult of the Barred Warbler has been published, neither from summer nor winter quarters. In this paper we present data showing that Barred Warblers have a moult pattern not previously described in any European passerine.

Methods

Barred Warblers were studied in the summers of 1985–1987 at Ottenby in southeastern Sweden (56° 12'N, 16° 24'E) in an area characterized by deciduous forest surrounded by shrubby grassland. The main breeding and moulting area of the Barred Warblers is the forest edge, an area dominated by bushes of *Prunus, Crataegus, Rubus* and *Juniperus;* the breeding habitat has been more thoroughly presented by Aulén (1976). Adult birds were caught near their nests in late June to mid July. In 1985 and 1986 extensive mist-netting was carried out in mid July to late August. Nestlings were also ringed throughout the study. Nine birds caught in late May and early June at the bird observatory (two km to the south) are included in the analysis.

The following age symbols are used in this paper: ly – a bird in its first calendar year (Euring code 3), 2y – a bird in its second calendar yar (5) and 3y+ – a bird in, at least, its third calendar year (6).

Adults were aged and sexed according to criteria based on information in Williamson (1968), Schmidt (1981), Busse (1984), Svensson (1984) and own obser-

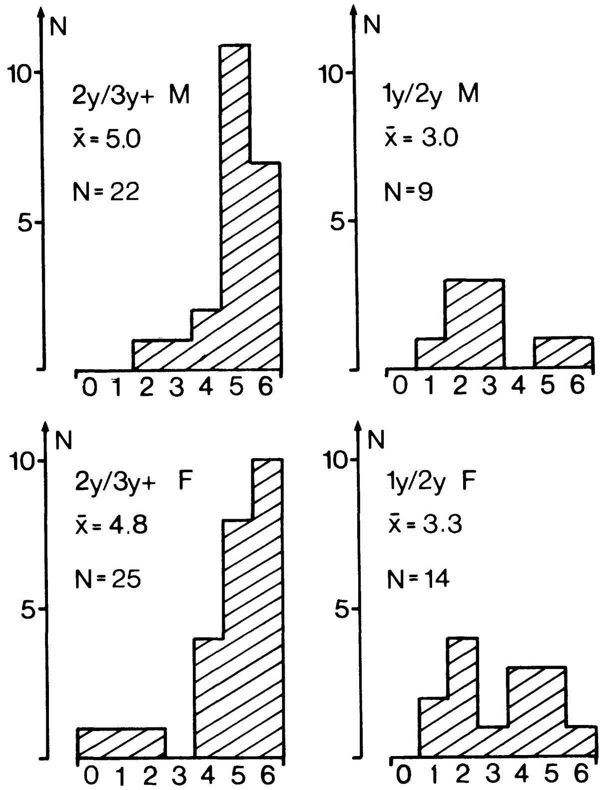

Fig. 2. The number of secondaries moulted during winter in each age and sex class. 1y/2y are birds in their first winter and 2y/3y+ are birds in their second or later winter. M = males, F = females.

vations. Breeding birds were sexed according to the incubation patch. Females have a wrinkled patch and males always have some downy feathers on the upper chest. We caught several pairs at their nests; there was always a clear, though small, difference between the sexes and we found no intermediates. A nice picture showing the difference can be found in Efremov and Payevsky (1973). Birds were aged mainly on eye-colour, colour of head and back and on the amount of barring on the underparts. Further, 2y birds have bluish-grey legs differing from the more yellowish-grey legs of 3y+ birds (as pointed out to us by L. Karlsson). Age criteria were checked against retraps of birds ringed as nestlings, juveniles (1y) and adults. A more detailed description of the ageing and sexing can be obtained from the authors.

The moult status of remiges and rectrices was closely examined and three categories of feathers were separated:

Old (O): Bleached and very worn feathers (cf. Fig. 1).

Winter shed (W): Clearly darker than O and only slightly worn feathers, normally with a white edge at the tip. Sometimes they differed in length from O and/or from each other (cf. Fig. 1).

New (N): Moulted in the study area during the year of investigation. Growing or just fullgrown, completely fresh and unbleached.

Moult was studied on the left wing (though both wings were checked on most birds) and active moult was recorded according to Ginn and Melville (1983). An unmoulted feather (here O or W) scores 0 and a fully grown feather (N) scores 5. Accordingly, a completely renewed wing has a primary score (PS) of 45 (the outermost minute primary is excluded from the analysis), a secondary score of 30 and a tertial score of 15. Primaries were numbered from the innermost towards the tip of the wing and secondaries and tertials from the outermost towards the body. Tail feathers were numbered from the central (1) to the outermost (6) feather. Moult duration for an individual bird was calculated by regressing date against PS (Ginn and Melville 1983).

Results

Moult of wing feathers

Moult in winter quarters

We interpret the normally clear-cut difference between O and W feathers as a result of a moult carried out away from the breeding grounds, most certainly in the winter quarters. The often irregular pattern (e.g. secondaries 1, 2 and 6 as W and secondaries 3, 4 and 5 as O) rules out the possibility that the difference should be due to wear. Moreover, we caught some individuals in two successive years and many of their secondaries were fresher in spring than they were when they left the previous autumn.

Feathers that we classified as W were normally only slightly worn and bleached, indicating that they had been replaced just prior to spring migration. In some cases there was a cline in wear of the W feathers, probably due to a prolonged moulting period. In a few cases we were uncertain whether a particular feather was W or O (i.e. where the exact border between W and O was located). However, the classification of these few feathers will not alter the general significance and the interpretation of the results.

In the period away from their breeding grounds, Barred Warblers regularly moult some, or most of their secondaries (Fig. 2). Among 3y+ birds, 77% had moulted 5 or 6 secondaries (n = 47) while only 26% of the 2y birds (n = 23) had done so. The average number of winter shed (W) secondaries was significantly lower in 2y than in 3y+ birds (2y: $\bar{x} = 3.2$, 3y+: $\bar{x} = 4.9$; $p < 0.001$, Mann-Whitney U-test). Differences between sexes within age groups were not significant (2y:

Tab. 1. Number of individuals in each age and sex class that had moulted a certain wing feather in winter and summer, respectively (e.g. among 14 1y/2y females examined for winter moult, 9 individuals had moulted secondary 6, 10 had moulted secondary 5, and so on). As far as summer moult is concerned, only birds with a primary score of 35 or more are included. Age and sex symbols as in Fig. 2.

		Tertials			Secondaries						Primaries								
	N	3	2	1	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9
Winter moult																			
1y/2y M	9	2	1	1	7	8	3	3	2	4	–	–	–	–	–	–	–	1	2
1y/2y F	14[a]	1	3	1	9	10	9	6	6	6	–	–	–	–	–	–	1	2	3
2y/3y+ M	22	1	2	3	13	22	21	20	19	15	–	1	–	–	–	–	–	1	1
2y/3y+ F	25[a]	3	3	3	14	24	23	21	20	17	2	–	–	–	–	–	–	–	–
Summer moult																			
2y M	3[a]	1	1	1	–	1	2	2	2	2									
2y F	4	4	4	3	–	–	–	–	–	1									
3y+ M	3	3	3	3	–	–	–	–	–	1					All moulted[b]				
3y+ F	6	5	6	6	–	1	–	–	2	2									

[a] In one of these birds moult status of tertials was not examined.
[b] There were no indications that any bird left any primaries unmoulted.

p>0.05, 3y+: p>0.05, Mann-Whitney U-test). We found no ly birds moulting any wing or tail feathers before the autumn migration (n = 46).

In 50 birds, the number of winter replaced secondaries was checked in both wings. This number was the same in 30 individuals, differed by one in 16 individuals and by two in four individuals. However, four of the 30 individuals with an equal number of winter secondaries showed asymmetric moult.

The 2y birds had most often renewed the two innermost secondaries (5 and 6). Almost all 3y+ birds had renewed secondaries 2–5, but only about 50% had moulted the innermost secondary (6). A few birds also had some fresh (W) primaries (mainly in first winter birds) and/or tertials (Tab. 1).

Moult in the breeding area

The general, summer moult of adults includes all primaries and tertials but none, or just a few, of the secondaries (Tab. 1). Primaries were moulted in the normal passerine sequence, i.e. from the innermost towards the tip of the wing.

Regressing date on PS gives a duration of primary moult of 45 d for the individual bird (Fig. 3). However, as some birds (of both sexes) shed one or two of the innermost primaries while still feeding their young, their moult duration becomes longer than that of birds which did not start moult until their young were independent. The latter group commenced their moult by shedding 4–5 inner primaries per wing simultaneously.

The average moulting rate of individuals captured and recaptured on dates at least 10 d apart was 1.22 points d^{-1} (SD = 0.28, n = 5); this would correspond to a duration of 37 d for complete primary moult. There were no apparent intersexual differences in the timing of moult initiation, nor in moult duration (Fig. 3).

The earliest actively moulting bird was encountered on 23 June and the latest on 20 August with a PS of 42. Hence, moulting birds were present for a period of at least 58 days. Only two birds caught had completed moult and had all primaries fully grown. It was concluded that primary moult duration is approximately 40 d in the individual and that the whole population moults in about 60 d.

Only one bird was caught with a PS between 15 and 30, though trapping efforts were held constant during this period. Birds may become almost flightless at this stage of moult. Some individuals had 7–8 primaries growing simultaneously.

No secondaries were found to be shed after a PS of 35. By this PS, 3y+ birds had renewed on average 0.7 secondaries (n = 9) and 2y birds 1.4 (n = 7). The differ-

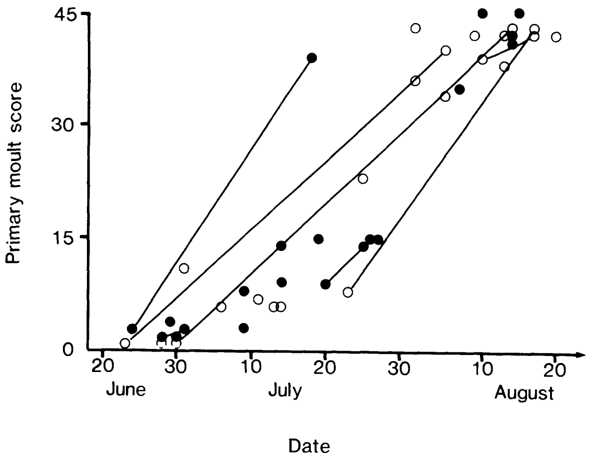

Fig. 3. Primary moult score against date for male (filled circles) and female (open circles) Barred Warblers at Ottenby, SE Sweden, in 1985 and 1986. Lines connect moult scores of individuals examined more than once.

Moult period	Tertials 9 8 7	Secondaries 6 5 4 3 2 1	Primaries 1 2 3 4 5 6 7 8 9	Recording date
Winter 1985	○ ○ ○	● ● ● ● ● ●	○ ○ ○ ○ ○ ○ ○ ○ ○	24 June
Summer 1985	● ● ●	○ ○ ○ ○ ○ ○	● ● ● ● ● ● ● ● ●	7 August PS 35
Winter 1986	○ ○ ○	○ ● ○ ● ○ ●	○ ○ ○ ○ ○ ○ ○ ○ ○	23 June
Summer 1986	● ● ●	○ ○ ○ ○ ○ ○	● ● ● ● ● ● ● ● ●	14 August PS 42

Fig. 4. The wing feather moult in a 3y+ male Barred Warbler in two successive years. Solid symbols denote moulted feathers and open sumbols denote unmoulted feathers. PS stands for primary score when examined.

ence is not statistically significant ($p > 0.05$, Mann-Whitney U-test). Seven out of these 16 birds (44%) moulted one or more secondaries. One 3y+ male moulted secondary 1 and two 3y+ females moulted secondaries 1,2 and 1,2,5, respectively. One 2y female moulted secondary 1 whereas three 2y males moulted secondaries 2,3; 1,3,4; and 1,2,4,5, respectively.

Tertials were moulted in the sequence 2-3-1 and moult was completed before primary moult completion. One bird had finished tertial moult at PS 35 and five birds at PS 42.

Annual moult patterns of known individuals

In those nine cases where the same individual was examined both before and after summer moult, none renewed any W secondaries (out of 31 such feathers). However, one 2y female renewed one W primary and one W tertial. The number of W secondaries in individuals varied between years. One 2y female moulted 2 secondaries in her first winter and 5 in her second winter. Another 2y female moulted 5,1 and 6 secondaries, respectively, in three consecutive winters. Four 3y+ males varied the number of secondaries moulted in winters as follows: 4,5; 6,4; 6,3; and 5,?,5.

For one 3y+ male, plumage records are available from both June and August (i.e. before and after summer moult) in two successive years (Fig. 4). This individual follows the general pattern found in the population. Primaries and tertials are moulted just after breeding, and secondaries are moulted in winter, though not all secondaries are renewed annually.

Moult of tail feathers

Barred Warblers arriving at their breeding grounds showed a varying number of W tail feathers (Tab. 2). 2y birds seemed to have renewed on average 9.4 ($n = 16$) tail feathers in their first winter. Among 3y+ birds, only on average 3.9 ($n = 34$) tail feathers were classified as W.

In summer, 2y and 3y+ birds renewed on average 3.3 ($n = 6$) and 3.9 ($n = 9$) tail feathers, respectively. When analysing post-breeding tail moult we only used birds with a PS of 35 or more as no tail feathers were found to be shed after that stage of primary moult.

Discussion

Adult post-breeding moult in the Barred Warbler has been reported to be complete (e.g. Witherby et al. 1943). Fracasso (1985) argues that after breeding all primaries and tertials, but only a few secondaries are moulted. Some data can be found on winter moult. According to Witherby et al. (1943), Williamson (1968) and Schmidt (1981) some individuals renew a few secondaries and tail feathers between December and April. In Kenya, this moult takes place in December-February (Pearson 1978). Studying circannual rhythms of moult in caged juvenile Barred Warblers, Berthold (1987) found an "umfangreiche Grossgefiedermauser" in February-May during their first winter but did not specify which feathers were moulted.

The summer moult strategy reported here is further supported by two birds from Lake Kvismaren in South Central Sweden. Of the wing feathers, only primaries and tertials were moulted after breeding (J. Sondell in litt.). Furthermore, W secondaries were recorded in four Barred Warblers caught at Falsterbo during the springs of 1985–1987. One 3y+ male had secondaries 2–5 new, one 3y+ female had secondaries 2–6 new while two 2y females had both moulted only the innermost secondary (L. Karlsson in litt.).

Tab. 2. The number of individuals that had moulted a certain tail feather during winter (feather classified as W) and summer moult, respectively. Males and females are treated together within each age class as differences between sexes are slight. Age symbols as in Fig. 2.

Season	Age	N	Rectrices											
			6	5	4	3	2	1	1	2	3	4	5	6
Winter	1y/2y	16	12	14	14	15	9	9	9	11	16	14	15	13
Aummer	2y	6	–	–	–	–	3	6	6	2	–	1	1	1
Winter	2y/3y+	34	14	12	11	11	9	9	3	11	12	13	12	17
Summer	3y+	9	2	–	2	2	2	9	6	5	4	1	–	2

The separation of three generations of feathers enables us to describe the year-round wing and tail moult of the Barred Warbler using data from just one locality. Most certainly, it is the late timing of the winter moult that makes it possible to separate W feathers. Our study shows that the Barred Warbler has divided its wing and tail moult into two stages, but the pattern is still not clear in detail . D. J. Pearson (in litt.) states that Barred Warblers in Kenya renew *all* tertials and most or all of their tail feathers in January-February and that fast wear possibly make tertials and central tail feathers look O already in June. Then, Barred Warblers would moult tertials and central tail feathers twice a year, though this is somewhat contradictory to the two clearly separable generations of tertials and tail feathers that we found in birds examined in June (cf. Fig. 1). However, the year-round moult pattern of primaries and secondaries described in this study is supported by observations from Kenya (D. J. Pearson in litt.).

One peculiarity of the Barred Warbler's moult is that some 2y birds (5 out of 23) moulted 1–3 outer primaries in winter. Such a moult in some first winter birds is also reported by Pearson (1978), and is possibly carried out in order to improve flight capability for the spring migration. This is a moult strategy similar to that found in many first winter Palaearctic waders wintering in Africa (Ginn and Melville 1983). Adult River Warblers moult their outer primaries upon arrival in Africa in autumn which is interpreted as a preparation for the next long migration further south (Pearson and Backhurst 1983).

The most noteworthy feature of the special moult of the Barred Warbler is that the first wing feathers that are regularly moulted in young birds are the secondaries, which are moulted in the winter quarters. As far as we know, this is unique for European passerines, though possibly found in some juveniles of the Asian White-throated Robin *Irania gutturalis* (Svensson 1984). As the secondaries normally are the least worn among the wing feathers in passerines, we do not believe that abrasion is the reason for them to be moulted first. Moreover, if priority was given to flight performance, moult of outer primaries, and not secondaries, should be favoured.

The renewal of the least exposed wing feathers in juveniles shows that the seasonally divided flight feather moult in the Barred Warbler is actively initiated already in the first winter. Therefore we consider the described moult pattern to be clearly different from the two main moult patterns found in European passerines.

What could be the selective advantage of this winter moult of secondaries by first year birds? After breeding, 2y and 3y+ Barred Warblers are able to start their autumn migration without having to moult many secondaries. Primary moult is so fast that near-flightlessness probably occurs and they leave just after moult completion. We interpret this as an urge to migrate as soon as possible. Then, winter moult of secondaries in juveniles (1y/2y) might be a preparation for the rapid summer moult. Otherwise 2y birds would have to make three long migrations on the same secondaries which probably would be disadvantageous. By starting to moult already in their first winter they can make this third journey with on average only 1.4 old secondaries and yet leave as early as the 3y+ birds do. Berthold (1979) found that among caged juveniles (1y) of eight *Sylvia* species, Barred Warblers had the earliest onset of migratory restlessness in autumn. Possibly, this preprogrammed urge to leave early, apply to adults (2y and 3y+) as well.

Why then, do the Barred Warblers leave so soon? This is a relevant question also in several other European passerines, in which the adults leave their breeding area much earlier than either the food or weather situation force them to, e.g. warblers of the genera *Locustella, Acrocephalus* and *Hippolais* and some other species wintering in the tropics. However, these species postpone all wing and tail feather moult until winter. The Barred Warbler seems to make a compromise between summer and winter moult. To understand the seasonally divided moult in this species, we must know the ecological factors leading to either summer or winter moult in passerines wintering in the tropics, factors that are still poorly known (Alerstam and Högstedt 1982). The moult pattern of the Barred Warbler indicates that for this species it is important to leave the breeding grounds soon after breeding, due to conditions either at the breeding grounds, along the autumn migration route or at the wintering grounds.

In the genus *Sylvia* there are now three clearly separated moult patterns known. Possibly, further studies of the ecology of birds of this particular genus, especially in wintering areas, might be fruitful when clarifying the adaptive significance of the different moult strategies found in European passerines.

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