THE MOLT OF THE EUROPEAN WHITETHROAT

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This paper describes molt in relation to migration in the European Whitethroat (*Sylvia communis*) in the western part of its range. The molt of this species has been described briefly by Williamson (1968), but this paper considers the molt in greater detail. At least in the subspecies *communis*, the molt is postnuptial; first-year birds do not molt the wing and tail feathers. First-year and adult birds are easily distinguishable in the hand by a variety of characteristics. This paper suggests that some adults do not complete their molt in one year, at least in Europe. These adults migrate with arrested molt, a condition in which the secondaries and rectrices have not been completely renewed. From this study I suggest that this is an adaptation to an unpredictable food supply.

MATERIALS AND METHODS

The data for this study are from two principal sources. The first, the collection of molt cards from the British Trust for Ornithology (B. T. O.) molt inquiry up to the end of 1968, comes principally from the Bird Observatories of Dungeness (Kent), Spurn Point (Yorkshire), and Gibraltar Point (Lincolnshire) and in smaller numbers from banders elsewhere in England. The second source is data collected by the author, during the autumn of 1967, on the Coto Doñana, Huelva, Spain.

At various stages throughout the paper, the terms primary, secondary, and tail score are used. These scores are obtained from the sums of the individual scores, each feather being scored as follows:

0 for an old feather
1 for a missing feather or one in pin
2, 3, 4 for feathers ⅓, ⅔, ⅔ of their normal length.
5 for a new feather, once its waxy sheath has been lost.

This means that the maximum scores are 50, 30, and 30 for the primaries, secondaries, and rectrices, respectively. This paper considers only primary, secondary, and tail molt since, until recently, body molt in the absence of wing molt was specifically excluded from the B.T.O. inquiry (Snow 1967).

RESULTS

DATA ON MOLT IN SPAIN

During September and early October 1967, 159 adult Whitethroats were caught on the Coto Doñana. Only two were in active molt, with primary scores of 48 and 48, and these had arrested secondary molt. Sixty-four of the birds (40%) had complete primary molt but incomplete and arrested secondary molt. Least squares correlation analysis of the secondary score against date shows little increase in molt score with date, and the percentage of birds with arrested molt does not decrease significantly with date ($\chi^2 = 1.5$, d.f. 3, $P = 0.7$; for four 5-day periods).

It appears that (1) no secondary replacement occurred while the birds were on the Coto Doñana; (2) the population as a whole was not replacing secondaries in areas through which they were migrating; and (3) these birds would presumably arrive in their winter quarters with arrested molt. It is not known where these individuals breed, but this may be in areas where the population tends toward the eastern European subspecies *icterops*; a group that completes much of the molt in its winter quarters (Stresemann and Stresemann 1968). The Whitethroat has a marked migratory divide, the birds from eastern Europe migrating via the eastern end of the Mediterranean rather than via Iberia. Banding recoveries show that the birds migrating through Iberia are from the British Isles, Belgium, Switzerland, France, and Germany as far as 10° E, and not from the area where *icterops* is known to occur. Table 1 shows the date and latitude of recoveries in Iberia of Whitethroats banded as adults (or at any age) in Britain and recovered in subsequent autumns. By early October eight birds were recovered as far south as the Coto Doñana, representing 14% of the recoveries in that period. At least a proportion of the birds caught on the Coto Doñana is likely to be of British origin, and the inference is that some of these would have arrested molt. In this case Whitethroats from Britain would go all the way to Africa with incompletely molted plumage. Yet very few if any Whitethroats with arrested molt have been found in Britain. Evidence will now be presented that these statements are, despite appearances, compatible, and that they have interesting implications.

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TABLE 1. Recoveries at different latitudes of adult Whitethroats banded in Britain.

Latitude (Iberia)	Date in ⅓ monthly periods											
	July	August			September			October			November	
	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd	3rd	1st	2nd
44–42°N		1			5	3	3(1)[a]	1			1	
42–40°N				1	3	6	9(2)	5	2			
40–38°N						6	1	1	2			1
38–36°N (Coto Doñana)	1				1	1	1(1)	2	2	1(2)		
South of 36°N							1		1			

[a] Numbers in parentheses represent birds for which the exact date is unknown.

THE TIMING AND DURATION OF THE MOLT OF BRITISH BIRDS

The molt of the primaries takes place during July, August, and September, its finish roughly coinciding with the migration (= departure) of Whitethroats as recorded at seven British Bird Observatories (Davis 1967).

Table 2 shows the time for a given score increase for individual primaries, secondaries, and rectrices from the retrap data. Within the limits of the method, the times for a given increase are reasonably constant, and there is little difference in the time required to grow any feather, be it the short primary 10, the long primaries 7 and 8, or any of the secondary feathers. Figure 1 shows the primary score against date for retrapped birds, and the mean scores for 5-day periods for individual observations. Least squares correlation analysis of the data gives a value of 51 days for the duration of the primary molt. The retrap data show a remarkably constant rate of molt between primary score values of 5 and 45, suggesting a duration of about 40 days. The discrepancy is probably due to the sigmoid nature of the molt score-date relationship. The rate of feather growth of each primary is similar (see table 2), so the primary score cannot increase as fast when only one feather is in growth, for instance at the beginning and end of molt, as during the middle of molt when, say, four feathers may be growing at once.

Figure 1 also shows the secondary score against dates for individual birds and retraps. Least squares correlation analysis of these data suggests a duration of the secondary molt of only 20 days, while retrap data, ignoring the possibly sigmoid nature of the molt, give a minimum value of 30 days for those individuals. A consideration of the plot of primary against secondary scores (Fig. 2) suggests a roughly equal increase in these values, hence 30 days would be correct for secondaries if 50 days were correct for the length of primary molt. This is consistent with the data in table 2. The correlation of primary molt with date is expressed by $r^2 = 0.76$, $n = 277$. This is good compared with that for the secondaries against date, $r^2 = 0.42$. Its relevance is discussed below.

Figure 1 also shows the tail score against date, giving a value of 32 days for the duration of the molt; retrap data are not shown. The

TABLE 2. Times for growth (in days) between various stages of individual primary, secondary, and tail feathers; since exact dates of onset and completion are not known, only minimum figures in each class have been used; only these are likely to approximate to the real values.

Feather type		Molt stage of each feather		
		0–3	0–4	0–N
Primary No.				
1		—	—	—
2		—	—	35
3		—	—	34
4		—	—	25
5		—	25	22
6		25	22	33
7		22	25	35
8		25	33	—
9		25	—	—
10		33	—	—
	Mean	26	26	31
Secondary No.				
1		25	22	25
2		—	34	25
3		33	—	25
4		—	25	—
5		33	—	—
6		25	—	33
	Mean	29	27	27
Tail No.				
1		—	—	25
2		22	25	25
3		25	22	25
4		25	—	34
5		11	—	34
6		—	34	34
	Mean	21	27	29

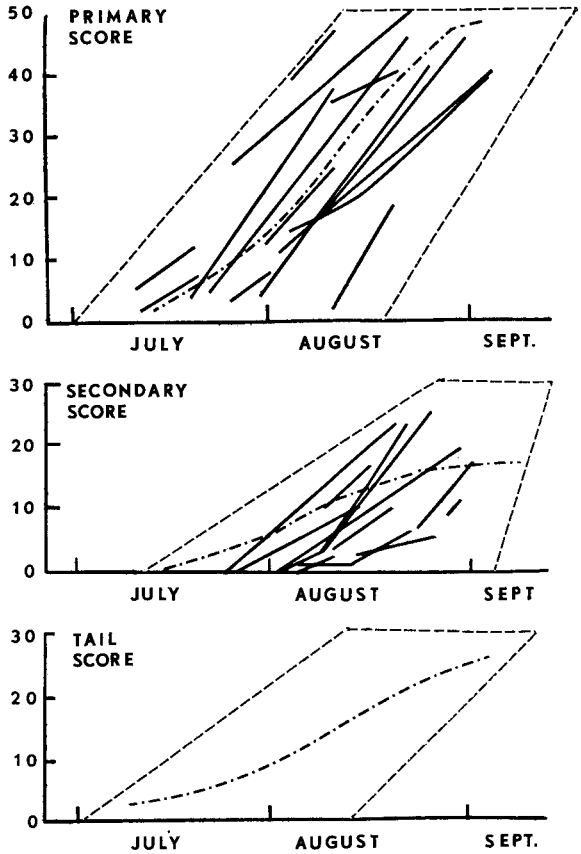

FIGURE 1. Primary, secondary, and tail scores plotted against date. The solid lines represent retrap data, the outer broken line represents the approximate limit of scatter, and the inner broken line, the mean score per 5-day intervals.

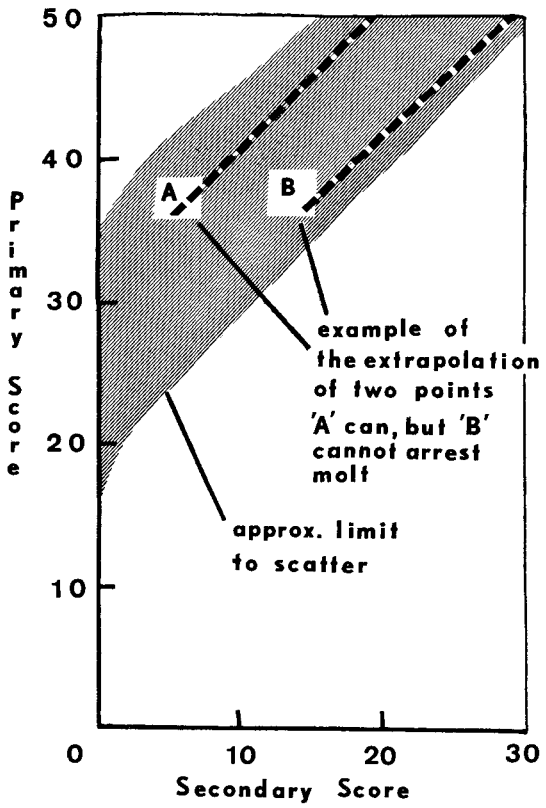

FIGURE 2. Primary score plotted against secondary score, to show examples of the extrapolation described in the text.

majority of the birds finish their tail molt by the first week of September.

THE RELATIONSHIP OF PRIMARY MOLT TO SECONDARY AND TAIL MOLT

The relationship between primary and secondary molt is such that molt of the secondaries usually begins when the primary score is between 20 and 30 (fig. 2). The relationship between primary score and the corresponding tail score is such as to indicate that the tail begins to molt earlier than the secondaries and usually finishes before them.

Since the average rates of increase in primary and secondary scores are known, each observed point can be extrapolated to the point where the primaries have finished, and the corresponding value for the secondary score can then be obtained (see fig. 2). Doing this for all the values of primary and secondary scores observed gives an estimate of the percentage of the population which will finish their primaries before their secondaries. This can be repeated for the rectrices. When the primaries are complete, but the secondaries or tail feathers are incomplete (as deduced from the extrapolation), if the molt was arrested, we have an estimate of its occurrence in the population. The results of this procedure are shown in table 3. The rates of increase in scores used for this analysis are 51 days for primary molt (from regression analysis), 30 days for secondary molt (the value obtained from the least means squares correlation is impossible for all the retraps and there is reason for doubting it—see below), and 32 days for tail molt. The regression value for the primaries is likely to be more accurate than the retrap value since most of the points are at the beginning and the end rather than in the middle (across which the retraps extend) of the molting period.

Table 3 suggests that a considerable proportion of birds could have completed their primaries while their secondaries were incomplete. The percentage of birds which finish their primaries while the secondaries had less than a score of 25 is 39%, nearly the same figure as the percentage of birds caught on the Coto Doñana with arrested molt. How-

TABLE 3. Numbers of British-caught Whitethroats at the stage at which primary molt might be expected to have finished; calculated from extrapolation of the data on the basis explained in the text.

	Secondary molt							
	Score						Secondaries before primaries	Total
	0–5	6–10	11–15	16–20	21–25	26–30		
No. finishing	0	2	11	29	66	152	17	277
% of total	0	1	4	10	24	55	6	100
		39% could arrest molt						

	Tail molt							
	Score						Tail before primaries	Total
	1–5	6–10	11–15	16–20	21–25	26–30		
No. finishing	2	2	4	2	3	23	278	314
% of total	1	1	1	1	1	7	89	101
	5% could arrest molt							

ever, this figure is subject to certain sources of error:

1. The percentage would be greater if a higher rate of secondary molt was used in the extrapolation and reduced if a higher rate of primary molt was used.

2. Some birds may be unable to arrest their molt. For example, if the secondary score was 25 when the primaries were complete, this may have been due to retention of one old feather and the bird need not replace it; or, it may have been due to one new feather and five feathers each nearly, but not quite, completed, a situation in which the bird could not arrest its molt.

3. The value would be reduced if the birds could increase their rate of secondary replacement; yet retrap data from this and other species show no indication of this being possible. A slowing down of the replacement of the primaries would have the same effect; yet one would expect that any factor limiting the rate of primary replacement would also affect the secondaries, since birds are found with old secondaries and completed primaries but not vice versa.

4. A factor tending to increase the number of birds with arrested secondaries for a given molt score is the asymmetry of wing molt. (Asymmetry is found in over 50% of the birds.) A bird, for example, with a score of, say, 25 may be one of the majority of birds which appear from the extrapolations above to finish their secondaries first. Yet, this score may be the average of a complete secondary molt on one wing but only four new feathers on the other. Such a bird would be more than the expected 5 days in finishing its molt, and could arrest its molt.

However these factors interact, there is little doubt that a percentage of birds finish their primaries ahead of their secondaries and could have stopped actively molting their secondaries. Perhaps 5% of birds in which the secondaries are incompletely molted show no active molt of the secondaries, the primaries being complete or nearly so. This percentage is expected to be small since apart from banders being instructed to look only for active molt, it may be argued that molt is arrested so that migration can begin. Thus one would not expect to find them in Britain in this condition.

The presence in Britain of birds with incompletely molted secondaries does not mean that they leave in this condition; they may replace these feathers after the primaries have been completed. However, few if any birds have been found by British observers in this state. These birds and possibly those in Iberia could be molting at a slow rate, i.e., one feather is replaced before the next one is dropped. For birds with only one secondary growing, if the actual rate of feather growth remains constant (previous work suggests this), then a slowing of the molt can be achieved only by replacing fewer feathers at one time. To return to figure 1, just the opposite effect, i.e., a speeding up of the secondary molt, is required to prevent the possibility of arrested molt. While similar plots for the primaries and rectrices show a roughly parallelogram-shaped scatter, the scatter for secondaries is roughly trapezoid. This shape is reflected in the poor correlation of molt score with date. In fact, a parallelogram-shaped scatter is unlikely for even normal rates of molt, for some individuals would be finishing secondary molt in the second week of October. The trapezoid-shaped scatter can be explained in two ways: first, that in the beginning of September birds with low secondary

scores accelerate the rate of secondary molt; second, that after the first 10 days of September, there are no longer any numbers of birds with molting secondaries, that is, they have left the country. To explain the presence of arrested molt in British birds as a slowing down of the molt is clearly contradictory since birds late in the season can only either arrest their molt or speed it up. Thus the hypothesis that British birds arrest their molt is the only simple interpretation of the data.

Since tail molt is started much earlier than secondary molt, it tends to finish before the primaries finish, yet table 3 shows that not all do. For these, similar arguments exist as for the secondaries.

It would be advantageous if badly worn secondaries could be replaced first and so provide the best possible wing if the molt were not going to be completed. This fits with the good condition of the old feathers of the birds caught in Spain and their sometimes asymmetrical distribution between wings, but whether a bird can do this with what is essentially a dead structure is very speculative. No other reason for the asymmetry suggests itself.

DISCUSSION

So far there are no banding data, to my knowledge, that show the origin of the Iberian birds caught with arrested molt, or that show a British bird that has been caught outside Britain with arrested molt. However, there appears to be good evidence that British birds do not all have the time to complete their secondary molt in Britain and that, in areas where British birds are known to occur, such as in southern Spain, birds with arrested molt are found. The birds in southern Spain in 1967 appeared unable to complete their molt in Spain either. The conclusion drawn is that some British birds very probably complete their molt in the winter quarters, having gone there with arrested molt.

A migrant wintering in Africa and breeding in Europe has a "choice" between molting in Europe or Africa. In Europe the weather at the end of the breeding season may be unpredictable, affecting directly or indirectly the availability of the food, perhaps insects, needed for molt. In Africa, most palearctic migrants winter in the drier areas south of the Sahara (north of the tropical forests) when these areas are experiencing their driest period. These areas have a rich, resident avifauna, which, in addition to the other species of migrants, might be expected to provide serious competition to a bird in molt. Molt reduces a Whitethroat's thermal insulation and its ability to fly (judged by the relatively fewer birds caught in intermediate stages of molt than caught when starting or finishing molt), suggesting that the molting period may well be a critical one for this and other species. Arrested molt provides a mechanism whereby a bird does not have to complete its entire molt in Europe or Africa. It can start in Europe and, if conditions are bad there, finish in Africa. It is an adaptation which permits flexibility in the face of an unpredictable food supply. Birds late in finishing breeding, perhaps having arrived late on the breeding grounds, do not have to complete their molt during the time when the food supply can be guaranteed. An inflexible molt schedule might prevent a species from breeding late or from breeding in northerly latitudes where the summer season is short. With flexibility, if the food supplies do continue late into the autumn, the bird can complete its molt; if not, it can arrest its molt to finish it in Africa. (Birds are not found in active molt on migration.) Such an adaptation would be expected among birds in an unpredictable environment, including other trans-Saharan migrants. It has been recorded for other members of the genus (by the present author, quoted in Williamson 1968).

SUMMARY

The timing and duration of primary, secondary, and tail molt and their relation with one another are discussed, and the conclusion is drawn that some British Whitethroats leave the country with incompletely replaced secondaries. Other hypotheses are mentioned and the reasons for rejecting them are stated. Birds caught on the continent, in Iberia, with arrested molt were shown, at least in 1967, not to be replacing their old secondaries. Since areas in Iberia have produced recoveries of adult birds from Britain, it is thought likely that some British birds migrate to their winter quarters with arrested molt. The value of arrested molt is discussed.

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LITERATURE CITED

DAVIS, P. 1967. Migration seasons of Sylvia Warblers at British Bird Observatories. Bird Study 14:65–95.

SNOW, D. 1967. A guide to moult in British Birds. British Trust for Ornithology Field Guide no. 11.

STRESEMANN, E., AND V. STRESEMANN. 1968. Winterquartier und Mauser der Dorngrasmucke (*Sylvia communis*). J. Ornithol. 109:303–314.

WILLIAMSON, D. 1968. Identification for Ringers no. 3; the genus *Sylvia*. British Trust for Ornithology Field Guide no. 9.

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