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THE SPRING MIGRATION OF THE WILLOW WARBLER IN 1952.

BY

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INTRODUCTION.

THE study of bird-migration in the British area has received a great impetus since the war through the establishment of a number of bird observatories at widely separated points, the manning of these stations by competent amateur watchers during migration seasons, and the gradual development of new techniques of research. There is close co-operation and exchange of ideas between those who are responsible for organizing and carrying out this work, through personal contact at the meetings of the British Trust for Ornithology Bird Observatories Committee, and also through the pages of the *Fair Isle Bird Observatory Bulletin*, which is devoted to recording the detailed results from many quarters of this new approach to an old problem.

The present paper is an attempt to show to what extent this pooling of ideas and information, and the application of such new techniques of analysis as the bird observatories are developing, can be productive of results when applied to a specific problem in bird-migration—in this case, the pattern of the spring migration of the Willow Warbler (*Phylloscopus trochilus*) through the British Isles. The authors also hope that the paper may be viewed from a somewhat wider angle—namely, as a statement of the potentialities of this kind of co-operative analytical work, which we confidently hope will become increasingly efficacious as the scope and opportunities (at present restricted by the lack of finance, and in some cases of adequate supervision) of the various bird observatories improves.

In previous years each bird observatory has selected a species of migrant and, with the help of information supplied by the other stations, has attempted to work out the pattern of its movements through the British Isles. The results of these investigations for 1950 and 1951 were published in *British Birds* (see vol. xlv, pp. 236-245, and vol. xlv, pp. 245-256, 306-314 respectively).* For 1952 the present authors undertook to attempt an elucidation of the movements of the Willow Warbler, largely because it seemed likely that this abundant species, which has a widespread breeding-range in Europe, would present more difficulties than the comparatively scarce and local species such as Ring Ouzel

* A few investigations of this kind were continued for 1952 (*antea*, pp. 16-23).

(*Turdus torquatus*) and Red-backed Shrike (*Lanius collurio*) which we had dealt with previously, and thus provide a severer test of the validity of our methods. And, should the question prove too complicated for present analysis, it would be a distinct advantage to know just what the major difficulties were.

ACKNOWLEDGEMENTS.

We are grateful to a number of friends and colleagues for their help. Major R. F. Ruttledge kindly placed all his 1952 Willow Warbler data from Great Saltee at our disposal, and Peter Davis and Peter Conder were as generous with the Lundy and Skokholm records. Our thanks are also due to the Isle of May Bird Observatory and Field Station Committee for their assistance, and to Dr. K. B. Rooke (Portland Bill, Dorset), Ian Walker (Little Ross Lighthouse, Solway), Leslie Anderson (Rhinns of Islay Lighthouse), and a number of foreign correspondents for their help. These include Staffan Ulfstrand and Carl-Fredrik Lundevall (Sweden), Carl Adolph Blume and members of "Danish Bird Investigation" (Denmark), Dr. Holger Holgersen (Norway) and Dr. A. C. Perdeck (Holland). We thank H. O. Bunce for a translation of a Swedish paper.

TAXONOMIC.

Ticehurst (1938) has shown that it is possible to segregate the sexes of a large majority of Willow Warblers on the criterion of wing-length. He gives for spring birds of the typical race, *trochilus*, from the British Isles: ♂♂, 64-71.5 mm. but mostly 67-70 mm.; ♀♀, 61-65 mm., mostly 62-64 mm. He adds: "Central European birds (wing, ♂♂ 64-72.5, mostly 67-70) average a trifle larger in wing, but there is an 85% overlap." The German and south Swedish populations north to the great lakes Vänern and Vättern have been identified by some workers (Zedlitz, 1925; Salomonsen, 1928) with the form *Phylloscopus trochilus fitis* of Bechstein, but in view of the wide overlap in measurements and the lack of any constant plumage difference Ticehurst regarded *fitis* as a synonym of *trochilus*. In a subsequent study of the group Salomonsen (1945) concurred with this view.

North and east of the Swedish lakes, as pointed out by Salomonsen, the race *acredula* breeds. A difficulty we have met in this investigation is the question—what credence should be allowed to statements in bird observatory records that such-and-such birds are "Northern" or *acredula* Willow Warblers. It is probable that where *acredula* is mentioned the bird in question approximates to the brown-and-white eastern form *yakutensis*, birds similar to which are known to occur in north-east Sweden alongside typical *acredula*, from which they were formerly distinguished under the

name "*eversmanni*" (see the discussion in Ticehurst, *op. cit.*, pp. 28-9). There is evidence that at Great Saltee in the west and the Isle of May in the east *acredula* is a not infrequent bird of passage: the detailed observations of Ruttledge (1951, 1952), and the many specimens of *acredula* collected at the Isle of May in former years by the Misses E. V. Baxter and L. J. Rintoul (and now in the Royal Scottish and St. Andrews University Museums) lend strong support to this view. The same collections contain a number of *acredula* collected at Fair Isle by Dr. William Eagle Clarke and Surgeon Rear-Admiral J. H. Stenhouse, but in recent years we have found this race very rare in the spring passage through the isle.

This form intergrades in plumage with *trochilus* on the one hand and with the *yakutensis* or "*eversmanni*" type on the other. It is therefore quite impossible to identify trapped Willow Warblers exactly without comparing them with a carefully selected series of skins. Such material has been made available to the Fair Isle Bird Observatory through the good offices of Dr. A. C. Stephen of the Royal Scottish Museum, and for 1953 this courtesy was extended to Great Saltee. Pending a fuller examination of the matter, the status on passage of the "Northern" race has been left in abeyance, and we have excluded from this study any birds so identified on the grounds of a "brown-and-white" plumage pattern.

Comparison with skins of the birds trapped at Fair Isle in the spring of 1952 revealed that the passage was made up almost entirely of birds indistinguishable from the typical race. Only two *acredula* were trapped, on April 30th and May 13th.

METHODS.

The conclusions we have come to with regard to the migration of this species in spring 1952 are based partly on the statistical analysis of wing-length data, and partly on a correlation between observed movements of the Willow Warbler (and associated species) and the prevailing weather conditions. This study has involved the consideration of bi-modal distributions which do not lend themselves to exact or unique solutions. The solutions which we have adopted are not the only possible ones, but we believe that they are so close to the truth that any errors in them are negligible in comparison with the other errors involved in work which seeks to synthesize the efforts of so many individuals. Meteorological information has been obtained from the *Daily Weather Report* of the Meteorological Office of the Air Ministry, and we are grateful to the Controller of H.M. Stationery Office for permission to reproduce sketch-maps based on those in the *Report*. In interpreting the various situations, the concept of

migrational drift outlined by Williamson (1952, 1953) has been used as a working hypothesis.

A certain amount of corroborative evidence has been adduced from the weight-records. Our conclusions with regard to the significance of differences in the weight-records are based on our previous experience with other species, and in view of the general importance of this subject to migration analysis it is discussed in greater detail in a later section. Meanwhile, it should be emphasised that too little is yet known about the ways in which bird-weights vary to permit of their being used as other than supporting evidence, except in certain special cases.

As regards wing-length, it should be emphasised that the measurements were taken by a number of observers not all of whom may have used the same technique. A modification of the method described in *The Handbook* (Witherby *et al.*, 1938, vol. I, p. xxxiv) is used at Fair Isle and at most other bird observatories, in which the *minimum* wing-length is recorded, not the maximum: this gives equal reliability in the records and reduces the risk of injury to the bird as there is no need to put pressure on the carpalia. It is almost certain that a small degree of error is involved, but as more than one person was responsible at each of the observatories, and the number measured is so large, we feel justified in regarding this error as standard and in accepting the series as valid for the comparisons we have made.

It will be seen that the figures obtained at the bird observatories do not agree with those given by Ticehurst (1938) and Witherby *et al.* (1938) for the nominate race, but it must be remembered that whereas they measured study-specimens (in which some shrinkage of the wing always occurs) our own data are derived from the living bird. Those who have worked with both living and preserved material of any species will know that a discrepancy between the means of the two categories is to be expected, and will be on their guard when using the wing-lengths given in standard works as criteria for the separation of sex or race groups in observatory work.

THE SPRING MOVEMENTS.

A. *The Irish Sea.*

At Great Saltee the Willow Warbler migration was characterised by three peaks, a sharp one on April 9th (400 birds), a diffuse one on 15th (200) extending to 18th, and a more definite one on 24th-25th (100). At Lundy the first movements were on April 10th-11th (30 plus) and again on 13th (150), with another rise in numbers on 17th (80), and an increase on 23rd-24th (50) followed by "abundance" on 26th-27th. There were no important movements at either place in May.

Major Ruttledge informs us that there was a great rush of Willow Warblers for two hours early on April 17th at Inishtrahull

Lighthouse, Co. Donegal, and many were seen at the lantern of the Maidens Lighthouse, Co. Antrim, on the night of April 18th/19th (cf. the second peak at Great Saltee).

Between April 3rd and May 17th the wing-lengths of 329 birds were recorded at Great Saltee, a further 80 are available from Lundy, and 83 from Skokholm. Omitting the very few which were marked down as *acredula*, the Great Saltee data are summarized in Table I.

TABLE I.—DISTRIBUTION OF WING-LENGTHS OF WILLOW WARBLERS AT GREAT SALTEE IN APRIL AND MAY, 1952.

Wing-length in mm.	60	61	62	63	64	65	66	67	68	69	70	71	Total	
Apr. 3rd-Apr. 11th	...	0	0	1	2	2	5	8	17	17	18	6	0	76
Apr. 12th-May 17th	...	8	28	68	64	35	22	5	6	8	2	1	2	249
Total number	...	8	28	69	66	37	27	13	23	25	20	7	2	325

Wing-length in mm.	THEORETICAL DISTRIBUTION												Total				
	60	61	62	63	64	65	66	67	68	69	70	71					
♂♂	0	0	0	0	0	1	7	20	27	20	7	1	83
♀♀	8	28	58	70	50	21	5	1	0	0	0	0	241
Total	8	28	58	70	50	22	12	21	27	20	7	1	324

We see that, taken as a whole, the wing-lengths follow a bimodal distribution. The simplest explanation which suggests itself is that the birds in the lower part of the distribution are ♀♀, whilst those in the higher part are ♂♂. The whole can be represented reasonably well by the following two distributions: The

A. Mean wing-length 68.00 mm., s.d. 1.65, n 83, ♂♂

A. Mean wing-length 62.84 mm., s.d. 1.89, n 241, ♀♀

distributions defined by these parameters are given in the first two theoretical rows of Table I, whilst their sum is given in the last row. There is a probability of 0.90 that the actual and theoretical distributions differ only by chance. From this we may deduce that birds with a wing-length below 66 mm. are almost certainly ♀♀, and those above this size are ♂♂. Birds in the 66 mm. class are equally likely to be of either sex. The ranges of wing-length for the two sexes on this material may therefore be taken as: ♂♂, (65) 66-71 mm.; ♀♀, 60-66 (67) mm.

Returning to Table I, we see that there were 77 birds with wing-lengths of 67 mm. or over, and 13 with 66 mm. Taking 6 of the latter to be ♂♂ this gives 83 ♂♂ in all, of which 62 occurred in the first period, so that ♂♂ constituted about 80% of the birds captured between April 3rd and 11th. In contrast, only 8% of the birds measured on or after April 12th were ♂♂.

A very similar state of affairs was recorded at Lundy and Skokholm. These results are expressed in Tables II and III.

TABLE II.—DISTRIBUTION OF WING-LENGTHS OF WILLOW WARBLERS AT LUNDY IN APRIL AND MAY, 1952.

Wing-length in mm.	60	61	62	63	64	65	66	67	68	69	70	71	Total	
Apr. 8th-Apr. 11th...	...	0	1	2	0	1	2	0	3	4	4	1	0	18
Apr. 12th-May 8th...	...	4	8	13	9	11	2	4	4	3	3	1	0	62
Total number	4	9	15	9	12	4	4	7	7	7	2	80

Of 80 birds, 23 are judged to be ♂♂; of 18 birds taken up to and including April 11th, 12 are presumed ♂♂, while 13 of the remaining 62 are also ♂♂, giving 67% and 21% respectively.

TABLE III.—DISTRIBUTION OF WING-LENGTHS OF WILLOW WARBLERS AT SKOKHOLM IN APRIL AND MAY, 1952.

Wing-length in mm.	60	61	62	63	64	65	66	67	68	69	70	71	Total	
Apr. 3rd-Apr. 11th...	...	0	0	0	1	0	1	1	3	3	4	1	3	17
Apr. 12th-May 5th...	...	1	5	11	10	13	14	3	2	2	2	2	1	66
Total number	1	5	11	11	13	15	4	5	5	6	3	83

Of 83 birds, 25 are judged to be ♂♂; of 17 birds taken up to and including April 11th, 14 are presumed ♂♂, while 11 of the remaining 66 are also ♂♂, giving 82% and 17% respectively.

There is very close agreement between the data from Skokholm and those from Lundy and in the following discussion we shall refer to the Lundy results only. Data supplied by Dr. Rooke from Portland Bill relates to the period from April 24th to May 5th only. During this period 28 birds were taken of which only 4 or 14% measured 66 mm. or over.

B. *The North Sea.*

The two observatories whose records have been examined are the Isle of May in the Firth of Forth, and Fair Isle between Orkney and Shetland, 220 miles to the north. There were a few birds at the Isle of May on April 15th-16th and 18th, and 15 or more on 26th-27th. About 30 appeared on May 1st, increasing slightly on the next two days, declining on 4th, with a rush of over 500 birds following on 5th. A gradual decrease in numbers ensued, and only very small influxes occurred later, on 17th (12) and 20th (30). There was no significant movement at Fair Isle until May 5th (20), the fore-runners of a peak of 60-plus the next day. Another influx occurred on 12th (21), Willow Warblers decreasing afterwards.

At both stations the Willow Warbler passage was thus quite different from that at Lundy and Great Saltee, not only in so far as dates of the peak movements are concerned, but also in the times of appearance of the two sexes. The Isle of May records

show 255 birds measured during the period, of which 252 were also weighed, and it is interesting to note that this data show some disagreement (which is discussed below) with the data obtained from 26 birds at Fair Isle.

TABLE IV.—DISTRIBUTION OF WING-LENGTHS OF WILLOW WARBLERS AT THE ISLE OF MAY IN APRIL AND MAY, 1952.

Wing-length in mm.	60	61	62	63	64	65	66	67	68	69	70	71	Total		
April 10th-May 2nd	...	1	0	2	1	1	2	4	9	7	13	1	3	44	
May 3rd-May 30th...	...	9	22	46	46	34	24	10	7	7	2	2	2	211	
Total number	10	22	48	47	35	26	14	16	14	15	3	5	255

The distribution of wing-lengths recorded at the Isle of May is not so obviously bimodal as that obtained from the Saltee data, yet it is clearly of this type. A chi-squared test shows that there is a probability of 0.50 that the distributions postulated to represent the Saltee data differ only by chance from the Isle of May data. This is not such close agreement as was obtained from the former series, but it is close enough to suggest that there is no real difference between the stocks of Willow Warblers caught at the two observatories. It must be emphasised that there is no proof that the stocks are identical, but we feel safe in accepting this identity as a working hypothesis.

Again we see the partial segregation of the two sexes. Using the same ranges as before, there are 60 ♂♂ in the series, 35 being taken in the period up to May 2nd. There were thus about 80% ♂♂ in the first period and only about 12% thereafter. In comparing these figures with those for Great Saltee it should be borne in mind that the dichotomy of the data in each case was made on the basis of a change in the predominant sex and on no other factor.

Hence the arrival of birds at the Isle of May repeated, almost three weeks later, the pattern of sex distribution noted in the southern part of the Irish Sea.

TABLE V.—DISTRIBUTION OF WING-LENGTHS OF WILLOW WARBLERS AT FAIR ISLE IN MAY AND JUNE, 1952.

Wing-length in mm.	62	63	64	65	66	67	68	69	70	71	72	Total	
May 5th-May 11th	0	1	0	0	2	2	4	5	4	0	2	20	
May 12th-June 3rd	1	1	3	0	1	0	0	0	0	0	0	6	
Total number	...	1	2	3	0	3	2	4	5	4	0	2	26

Table V reveals a different picture. At the more southerly stations, females preponderate if the passage as a whole is considered (Great Saltee 74%, Lundy 69%, Skokholm 66%, Isle of May 76%), yet here we have only 22% if the same criterion is used

in sex segregation. The data available are too small to make definite conclusions possible, as it is virtually certain that another bimodal distribution is involved, but it suggests yet a further point of difference from the earlier sets; namely, that the whole pattern has been shifted upwards. No bird was taken at Fair Isle with a wing of less than 62 mm., yet such birds were not uncommon at other observatories during the period under review, and were recorded at Fair Isle in the spring of 1950 and 1951. Equally, birds with wings of 72 mm. were recorded only at Fair Isle, and these have not been recorded there in previous years.

So we must regard the passage at Fair Isle as being possibly of a different stock from that recorded farther south, and also from that recorded at the island in previous seasons. There can be no certainty, however, on this point, and in fact it is impossible even to give a satisfactory estimate of its probability.

C. Summary.

It will be seen that there was nothing at either of the North Sea stations to correspond with the first Saltee ♂♂ peak of April 9th, or the ♀♀ peak at Lundy of April 13th. The second diffuse passage of April 15th-18th, comprising a majority of ♀♀ in the Irish Sea, was simultaneous with a similarly diffuse movement of ♂♂ in the Forth. On April 26th-27th further ♂♂ were on the move at the Isle of May, whilst Great Saltee and Lundy showed peaks of ♀♀ birds. Passage thereafter was at the North Sea stations only, the flow of ♂♂ continuing on May 1st in the Forth area, then abruptly changing to a preponderance of ♀♀. Movement slackened on 4th and an immense rush of mainly ♀♀ birds followed on 5th. At Fair Isle, however, the arrivals which began on this day and culminated on 6th were preponderantly ♂♂, this sex continuing to pass until 11th, after which ♀♀ only were trapped.

THE METEOROLOGICAL CORRELATION.

During mid-April a vast anticyclone was established in southern Europe with conditions favourable for a large-scale migration of summer visitors bound for the British Isles and western Europe. On April 9th the Atlantic seaboard of Britain was under the influence of a depression centred a good way to the west of the Hebrides; the wind was S.E.-S.S.E. in western France on the edge of the high pressure system, and any overnight drift of birds in the sea-areas Biscay and Sole would be deflected towards the Irish Sea by a veer of wind in its southern approaches as they came within the sphere of influence of the depression. It is suggested that the first peak of predominantly ♂♂ Willow Warblers at Saltee on April 9th and at Lundy on 10th-11th (onward passage ex Devon and Cornwall) comprised birds which

had been travelling through the Iberian Peninsula and western France on the fringe of a broader movement which formed the vanguard of the west European breeding-stock (Fig. 1).

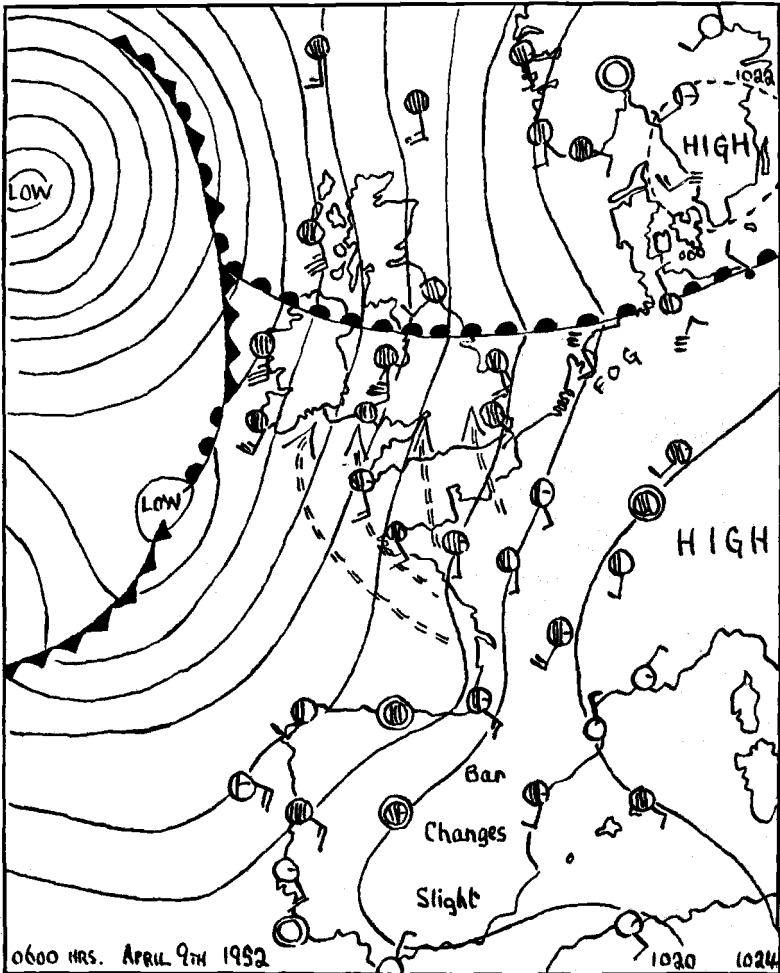


FIG. 1. WILLOW WARBLERS: ENTRY OF ♂♂ INTO SOUTHERN IRISH SEA, APRIL 9TH, 1952.

The passing of the warm sector of this low across England overnight on April 9th/10th deflected this movement to eastward, and on 10th the first Willow Warbler and other drift-migrants arrived at the Isle of May and the birds entered Denmark (see

below). Anti-cyclonic conditions spread to western France and Spain again on 12th/13th and a shallow low, covering Finistère and the West Country, with a S.E. wind in its warm sector, appears to have been responsible for the local peak at Lundy on 13th (Fig. 2). At this time calm anti-cyclonic weather was firmly

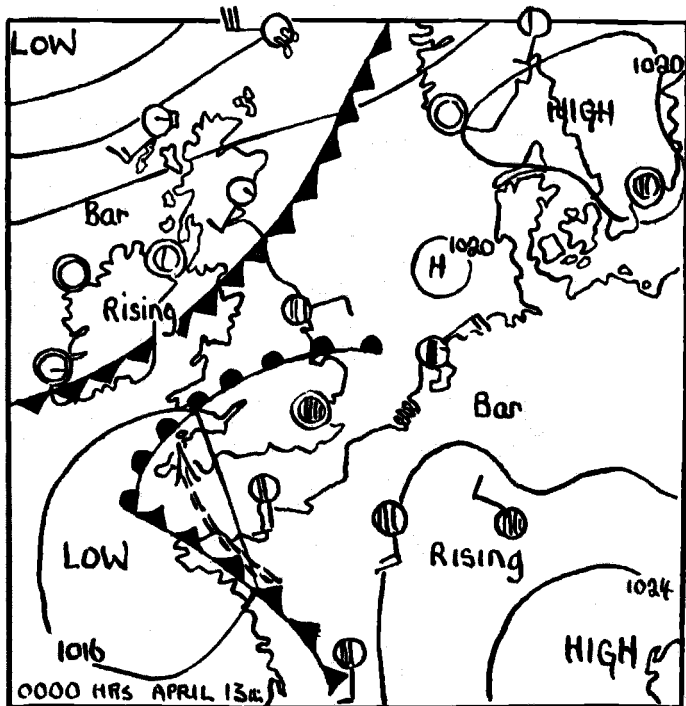


FIG. 2. WILLOW WARBLERS: LOCAL PEAK OF ♀♀, WEST OF ENGLAND, APRIL 13TH, 1952.

established over a wide area of western and central Europe, including the British Isles, and the first entry of ♀♀ at Great Saltee and the trickle of ♂♂ at the Isle of May beginning on 15th is correlated with the excellent passage weather then prevailing (Fig. 3a and b). Movement was also noticed at two west-coast lighthouses Little Ross (Solway) and Rhinns of Islay, as well as at the Irish light-stations previously mentioned. It is suggested that these again were birds of the British breeding-stock, the ♀♀ newly arrived in the south, the ♂♂ being the residue of the earlier entry of April 9th pursuing their northwood movement into Scotland.

This anticyclone retreated southwards during the night of April 18th/19th and first Scotland, and subsequently the whole of

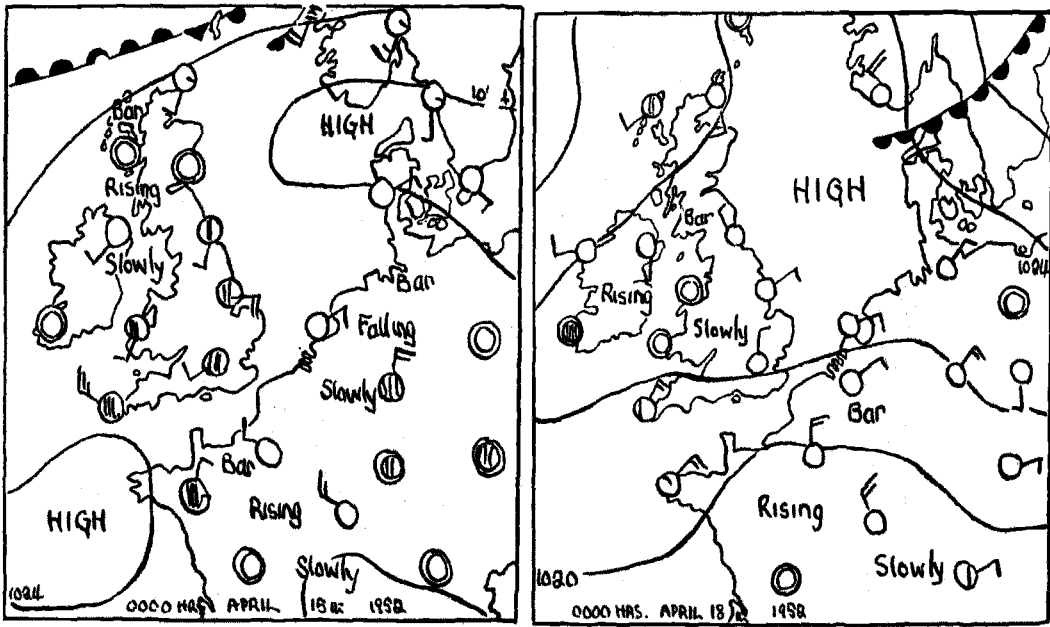


FIG. 3. WILLOW WARBLERS: ENTRY OF ♀♀ IN SOUTH AND ONWARD PASSAGE OF ♂♂ TO NORTH DURING ANTICYCLONIC WEATHER, APRIL 15TH-18TH, 1952.

Britain, came under the influence of a big depression which had approached Iceland from the west. This sudden change appears to have inhibited the migration urge, since movement ceased abruptly at the Isle of May, and was not resumed until 26th, about two days following the resumption of passage in the south-west.

This resurgence of passage, still of ♀ ♀ in the south and ♂ ♂ in the Forth, seems traceable to a return of anticyclonic weather, the ridge of an Azores high bringing calm or light wind conditions to the east coast of Scotland some 36 hrs. after its arrival in the south-west had released the final phase of ♀ ♀ movement there. The view that this movement was "onward passage" and not a result of drift is supported by observations of numbers of Willow Warblers at Little Ross and Rhinns of Islay on the other side of Scotland during the night of April 26th/27th. The approach of an active low to the south-west of Ireland on 30th brought this phase of the migration to an end.

From this point we are concerned only with movements affecting the North Sea coast of Britain. Anticyclonic weather, with generally clear skies and practically no wind except in the coastal regions, covered central and western Europe at the beginning of May, and North Sea winds were easterly on 1st on the northern side of a trough associated with the depression lying west of Ireland. Some of the Isle of May arrivals of May 1st were, we believe, drift-migrants from the Continent in this airstream ahead of a cold front; the occurrence of other migrants, including an Ortolan Bunting (*Emberiza hortulana*) (*antea*, vol. xlvi, p. 425) and Blue-headed Wagtail (*Motacilla f. flava*) supports this view. It should be noted that these birds, on the evidence of wing-length, were again mainly ♂ ♂.

This influx continued under similar weather conditions of a due easterly wind during the next two days, but with a sudden change in the distribution of the sexes, there being a preponderance of ♀ ♀ in the samples taken on 3rd and after. The Shetland region, with winds mainly north-east at this time, was beyond the effective reach of trans North Sea drift.

The great invasion of 500 plus, mostly ♀ ♀ in the Forth on May 5th was again due to migrational drift, this time across the northern perimeter of a low which had moved overnight from East Anglia into the North Sea (Fig. 4). The larger part of this drift must have crossed from the north-west German and Danish coasts ahead of the cold front, since behind this front the windstream was contrary. The few ♂ ♂ which reached Fair Isle almost certainly had a more northerly point of origin, which seems likely to have been south-west Norway, whence they were displaced by the easterly airstream ahead of the warm front on the northern periphery of the low.

It was not until next day, May 6th, that any number of Willow Warblers arrived at Fair Isle, and the cold front which had caused

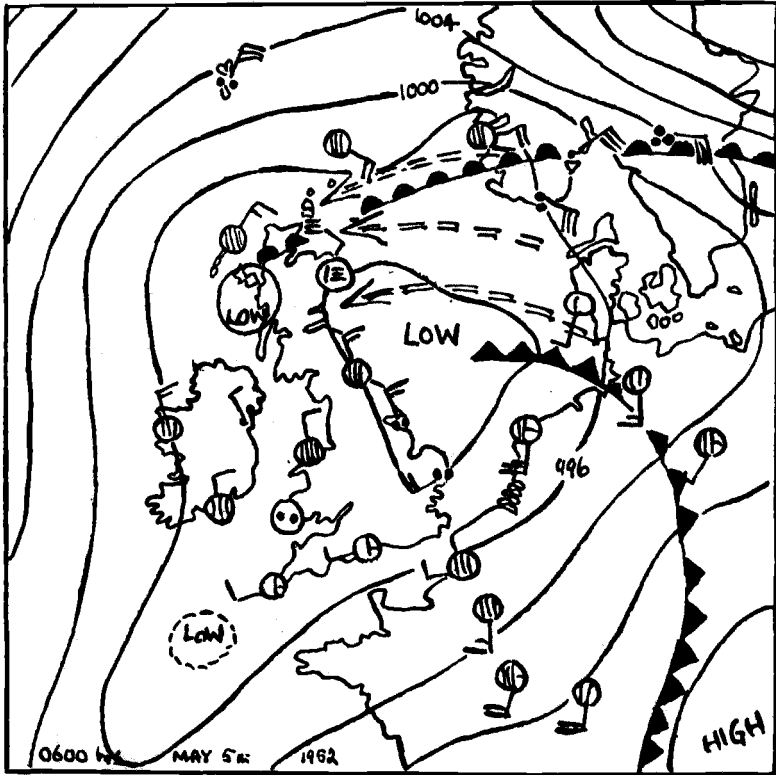


FIG. 4. WILLOW WARBLERS: RUSH OF 500 + ♀♀, ISLE OF MAY, WITH A FEW ♂♂, AT FAIR ISLE, MAY 5TH, 1952.

the previous night's drift to the Forth had by that time moved some 200 miles to the north. Thus the drift on this second night must have been largely composed of birds attempting to enter southern Scandinavia across the Kattegat and Skagerrak, for the wind-stream in that part of the North Sea to the south of the Skagerrak had veered south-west with the passing of the front and was no longer conducive to drift from the adjacent shores (Fig. 5).

Apart from a slight increase in Willow Warblers on May 9th, coinciding with an improvement in visibility after several misty days, there was no change of any importance till 12th, when a number of ♀♀ birds appear to have arrived from the Danish west coast or the Skagerrak round the northern side of a low centred over Caithness. The further movements at the Isle of May on 17th and especially 20th were probably due to passage

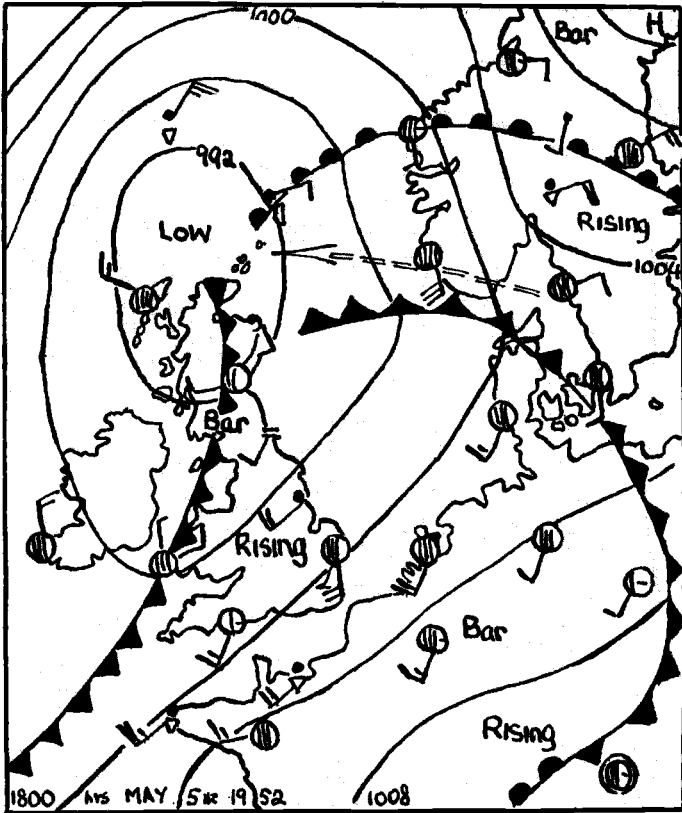


FIG. 5. WILLOW WARBLERS: DRIFT OF ♂♂ TO FAIR ISLE AHEAD OF COLD FRONT, OVERNIGHT, MAY 5TH-6TH, 1952.

continuing through Britain under anticyclonic conditions which have been described more fully in another connection (Williamson, 1953 b).

THE WEIGHT RECORDS.

The authors have already discussed briefly the difficulties which lie in the way of a valid interpretation of weight records in migration studies (Williamson and Butterfield, 1952). Their discussion presupposed a comparison in weights between birds assigned to "drift" and "onward passage" categories. A slightly different approach has been used (Butterfield, 1952 a and b) in which the weights of migrants arriving from overseas were compared with those of birds which could be assumed to have suffered little or no migration loss, e.g. birds whose journey had been over terrain which offered a succession of places close together suitable for

rest and feeding, or which had halted for a few days and had found opportunities to replenish their reserves of glycogen and fat. Such birds may be termed birds of "normal" weight, but even so the weight of any such individual will be liable to "local" fluctuations.

Fortunate circumstances during the spring of 1952 enabled us to make what is probably a reasonable estimate of the "normal" weight for this species, so we are able to make use of much of the weight data that is available. A combination of warm, damp, misty weather at Fair Isle in the second week of May induced birds of this species to stay on the isle for several days: there was a marked flush of insect-life, and wherever the grass was close-cropped numbers of Willow Warblers could be seen hopping about and feeding briskly very much after the manner of pipits. Some of these birds were re-trapped after the lapse of two or three days and showed considerable gains in weight, and in fact it seems reasonable to assume that they made good the losses which they had suffered during their North Sea drift. Summarised records of these birds are given below:

TABLE VI.—GAINS IN WEIGHT OF RE-CAPTURED WILLOW WARBLERS AT FAIR ISLE.

Date	First capture Time (G.M.T.)	Weight (gm.)	Date	Last capture Time (G.M.T.)	Weight (gm.)
<i>A.—Birds presumed to be ♂♂.</i>					
May 5th	1100	8.01	May 20th	1830	9.93
6th	0500	8.45	9th	1130	10.47
6th	0530	8.80	10th	0900	10.10
6th	0530	7.10	10th	1030	8.50
6th	1500	8.17	13th	0630	9.92
7th	1130	9.60	9th	1130	10.56
Mean weight		8.355	Mean weight		9.913
<i>B. Birds presumed to be ♀♀.</i>					
May 19th	1530	8.35	May 23rd	1030	9.09
21st	1500	7.87	23rd	1415	8.90

The birds taken between May 5th and 7th seem to have lost about 16% of their "normal" weight, which suggests that they had undergone a long oversea flight before arriving at Fair Isle, and which is inconsistent with the idea that they might have arrived from the mainland of Britain via Orkney. The remaining presumed ♂♂ of this period had a mean weight of 8.68 gm., not very different from the arrival-weight of the 6 discussed above. The 4 birds taken between May 8th and 11th were much heavier (mean weight 9.73 gm.) which suggests either that they had been on the island for at least two days before being captured, or that they had arrived from Orkney.

The large number of records (over 250) collected at Great Saltee presents a more stable picture suggesting several migratory

movements following each other under similar conditions. There are a few extraordinary records deviating markedly from the mean values of ♂♂ (8.90 gm.) and ♀♀ (7.92 gm.), which occurred as follows:

April 26th, ♀♀, 10.56 and 10.52 gm.

May 3rd, ♀♀, 5.23 and 5.15 gm.

May 15th, ♂, 10.13 gm.

The first four records were taken on days when many birds were recorded at more or less average weights. *It looks as though the first two and fifth of this series were birds which had spent a few days on the island or the adjacent Irish coast before being trapped, and had regained a "normal" weight.* If this is so, we may conclude that the majority of the Great Saltee birds had made an oversea flight of much the same duration as that of drift-migrants reaching Fair Isle.

On the Isle of May, 10 ♂♂ were taken between April 10th and 16th at a mean weight of 9.11 gm. In contrast, 16 ♂♂ trapped between April 18th and 30th had a mean of 9.93 gm. These values are sufficiently near the Fair Isle "drift" and "normal" values respectively (considering that the first class will generally have a shorter journey) to suggest that the birds passing through after April 18th were coastwise migrants and not arrivals from the Continent. The records for May 1st are conflicting: wing 69 mm. weight 8.6 gm.; wing 67 mm., 9.1 gm.; wing 69 mm., 7.1 gm.; wing 70 mm., 7.6 gm., and wing 67 mm., 9.8 gm. It seems likely that the first, third and fourth of these are drift-migrants and the fifth a passage bird; the second may also be passage, but its position is doubtful.

This day's records have been given *in extenso* to illustrate the difficulties in the way of weight analysis, and to indicate why we have felt that the labour of a full statistical treatment in the present study is not justified. A similar state of affairs is revealed by subsequent weight-records from the Isle of May. As stated earlier, ♀♀ preponderated there after May 3rd and the bulk of them appear to have been oversea drift-migrants of low arrival weight, with heavier birds scattered throughout the series which probably represent coastwise migrants or birds which had spent a few days on the island before being caught.

The chief value of this brief survey is to outline the way in which we believe weight records might be of some value in migration studies, and to show that in all cases the interpretation we have put upon the nature of the several movements from a study of the weather-charts is supported by the evidence of the weight records.

DISCUSSION.

The North Sea movements.

We have seen that an interpretation of the two big movements of May 5th and 6th in the light of the meteorological situation

shows that the Fair Isle fall must have originated considerably farther north than the Isle of May fall of the previous day. This conclusion, of course, is based on our acceptance of the principle that migrational drift is essentially down-wind. There are two facts which bring strong support to the view that on these two days different and widely separated points of origin were involved. Firstly, as has been shown, the Willow Warblers at Fair Isle were predominantly ♂♂ and not ♀♀ as had been the case in the Forth; and secondly, the whole composition of the rush was different at the two places, the May getting large numbers of Willow Warblers (500) and Whitethroats (*Sylvia communis*) (100), whereas the dominant species at Fair Isle were Tree Pipits (*Anthus trivialis*) (500) and Redstarts (*Phœnicurus phœnicurus*) (300).

Not only did this invasion of the 6th originate farther to the north, but there are also grounds for believing that it came ultimately from farther east than the previous day's fall, and represented, as it were, an entirely new 'migration-front'. For the previous ten days there had been a zone of high pressure over Italy, the Aegean and central Mediterranean, and it may be assumed that a very considerable north-westwards movement had been proceeding from this region through the col of fine weather which had existed since 3rd connecting this high with one situated over the Baltic States. Similar situations in previous seasons have led to big falls of migrants at points along the east coast (see *antea*, vol. xlv, pp. 248, 253, 261). The quite unusual strength at Fair Isle of two Scandinavian species which have a southern or south-eastern approach to their breeding-grounds—namely 15 Ortolan Buntings and 4 Wood Warblers (*Phylloscopus sibilatrix*) (*antea*, vol. xlvi, p. 424)—and the sight-record of a ♂ Grey-headed Wagtail (*Motacilla f. thunbergi*), are in keeping with this suggestion.

Thus the Willow Warblers at Fair Isle may have belonged to a more easterly population than those which sustained a drift off the north-west German and Danish coasts on the night of 4th/5th, —in other words, they may well have been birds of "fitis" stock moving into the Baltic States and southern Sweden. As "fitis" is slightly larger than true *trochilus* this could explain the fact that the wing-lengths of the Fair Isle ♂♂ slightly exceed those recorded nearly a month previously at Great Saltee, and are in excess of records we have taken in former years. But, as has been emphasized, the Fair Isle sample is too small to afford positive proof that a different stock of birds is involved.

Movement into Scandinavia.

It is worth while examining the situation in southern Scandinavia to see if any links with movements in the British area are apparent, and if there is any further support for the foregoing analysis. C. A. Blume writes that the first Willow Warblers

reached Denmark on April 10th, and adds that their arrival "never has taken place so early before, as far as we know." This date, it will be recalled, follows the main entry of ♂♂ into the southern Irish Sea, and coincides with the weather-change which brought the first drift-migrant Willow Warbler to the Isle of May. In Germany, 10 birds were singing at Neumünster, Holstein, on 11th, and by 13th the species was "everywhere" near the city of Schlesvig (J. Jørgensen). Numbers in Denmark built up during the following days and, according to Blume, nearly all the breeding-stock had arrived by April 20th. No birds were seen at Skagen, the northern tip of Jutland and an obvious jumping-off place for southern Norway, during a watch by Erik Hansen and others between April 10th and 15th. The first real indication of strong passage across the water-barrier to south-west Sweden seems to have been on May 1st, when 50 were counted at Søborg Mose, near Copenhagen, and 200 at the isle of Saltholm between Zealand and Sweden. It is clear that the movement of the species into Denmark kept pace with, and indeed may even have outstripped, the movement into Scotland.

There is, nevertheless, a distinct hiatus between the Willow Warbler occupation of Denmark and the entry into southern Sweden, judging by the information we have received from Staffan Ulfstrand,—who, together with B. Fritz, kept notes on arrivals in the Slotts and Öresunds parks in Malmö. Their observations began on April 15th, but beyond a continuous slight trickle there was no important influx until April 22nd. At this time Denmark was in the grip of a depression whose fronts were moving across the country, and a study of the weather-maps strongly suggests that these Willow Warblers entered Sweden in an easterly air-stream on the northern side of this low. There was no further influx on any scale until "huge numbers" suddenly appeared in the parks on May 5th, a day ahead of the rush at Fair Isle.

Ulfstrand (1952) has studied the movement of Willow Warblers into Sweden in previous years, using this method of daily counts in the Malmö parks. In 1949 the first wave was noted on April 24th, after which there was a slackening of activity until numbers appeared on May 5th-6th, together with Wood Warblers and Lesser Whitethroats (*Sylvia curruca*). In 1950 the main numbers were later than in either 1948 or 1949, this being true also for several other species, and it was May 1st before any quantity of Willow Warblers appeared, to be succeeded by a new wave on 10th.

There would seem to be some coincidence between the arrivals at Malmö, therefore, in 1948, 1949 and 1952, which suggests that this early May peak may approximate to the regular pattern. It is impossible, of course, to say anything about the distribution of the sexes in these movements, but it would seem probable—by analogy with the picture in the west—that whilst the vanguard of

the ♂♂ enter Sweden during the third week of April the peak invasion follows later, in the early days of May. Ulfstrand considers that this migration is derived from the south-east.

Progress of Willow Warbler migration.

Attention should be drawn to the relatively slow rate of progress of the Willow Warbler migration through the British Isles, where ♂♂ first appeared in numbers on April 9th, and had still not ceased to pass at the Isle of May by the end of the month. Moreover, ♂♂ of a similar south-western origin were still entering the Forth by drift from the Danish coast on May 1st, three weeks later, and both appear to have been rearguard movements, since there was a clear-cut change to birds of shorter wing-length a few days later. This indicates a very slow advance northwards, and it is interesting to observe the remarkable coincidence between this and the average rate of travel of 29 miles a day in the west postulated by Southern (1938). On this figure, we should expect the peak entry into the West Country and southern Ireland to be succeeded by a peak passage into Scotland, 500 miles to the north, some 17 days later: and, as we have seen, the dates corresponding to these peaks in 1952 were April 9th and 26th.

We now turn to a consideration of Southern's analysis of this bird's spring migration through Europe in the light of our own study. He attacked the same problem along rather different lines, by plotting mean arrival dates at many localities and connecting up the corresponding dates by a series of isochronal lines, drawn at fortnightly intervals. His map shows a distinct southwards bulge containing southernmost Sweden in the isochronal line for May 1st, a feature he was unable to explain, but which, we suggest, is further corroborative evidence that the birds entering Sweden do so from the south-east in the early days of May nearly a fortnight after the occupation of Denmark by ♂♂ of the south-western group. All the evidence suggests that the *trochilus* or "maritime" stock of Willow Warblers floods into Europe as far north as Scotland and Denmark (with perhaps some minor infiltration into southern Norway), the ♂♂ being in occupation in the third week of April; whilst the main body of the "fitis" or "Continental" stock flows northwards from Italy and the Aegean region, not reaching Sweden until the first days of May.

Weather and timing of migration.

Southern's work also established two other important characteristics of the Willow Warbler migration with which the conclusions we have reached from a study of our own data substantially agree. These are, firstly, an early entry via the Iberian Peninsula in the west followed by a marked "peripheral drive" in the early stages; and, secondly, a later start in the central and eastern Mediterranean countries with a correspondingly faster

rate of spread, so that the eastern populations gradually overhaul the western birds. As Southern points out, the run of the isochronal lines shows a remarkable conformity with the northwards movement of the spring isotherm: this, if not coincidence, would seem to indicate a correlation between the Willow Warbler's advance and the gradual increase in temperature over the continent. Ulfstrand (1952) has gone even further in an effort to establish a relationship between rising temperature and the Willow Warblers' arrival in Sweden.

This relationship, however, may be apparent rather than real, and it may be merely a secondary result of what is in our view the primary cause,—namely the development of sub-tropical anticyclonic weather in Europe in the spring. Such weather, in the extreme west of the Continent, is intermittent, since the polar front between the Continental and maritime air-masses, whose contrasting physical properties interact to cause low pressure disturbances, is normally located near the coastal regions. On the other hand, the Continental high is more stable. A study of the 1952 weather-charts shows that the migrants moving northwards from Italy and the Aegean region through central Europe had had anticyclonic weather or its equivalent—col conditions—almost uninterruptedly since the middle of April; and yet the main advance of the ♂♂ seems only to have drawn level with the rearguard of the coastwise-moving birds by May 5th. On the hypothesis that the stable conditions of anticyclonic weather, with light winds and clear skies, present the optimum opportunity for the movement of large numbers of birds, this can only mean that there must be a later entry into Europe on the part of the more easterly populations.

We suggest, therefore, that the evidence points to a marked physiological divergence of the two stocks, the "maritime" and the "continental" populations (or *trochilus* and "*fitis*" groups) as regards their migration programme, and that the former has evolved an earlier migration than the latter because it is forced to proceed at a slower rate owing to the less frequent development of anticyclonic weather favourable for migration through the coastal regions.

SUMMARY.

1. The course of the spring migration of the Willow Warbler (*Phylloscopus trochilus*) through Britain in 1952 is analysed, the study being based partly on a statistical examination of the wing-length records from several observatories, in order to assess the distribution of the sexes in the various movements; and partly on a correlation between the observed movements and the appropriate meteorological situations, using the theory of migrational drift as a working hypothesis. The records examined are those of Great Saltee, Skokholm and Lundy (southern Irish Sea), and Isle of May and Fair Isle (North Sea coast of Scotland).

2. The British breeding-stock entered the southern Irish Sea

in numbers from April 9th-11th (♂♂), April 13th and 15th-18th (♀♀) and April 26th-28th ♀♀). Movements at the Isle of May during the last two periods comprised the northward passage, in anticyclonic weather, of the residue of ♂♂ which had entered the south-west on April 9th. Later movements there, May 1st (♂♂) and 5th (♀♀), were due to migrational drift in easterly airstreams from the Continent. The only major influx at Fair Isle, May 6th (♂♂), was also a result of drift from southern Scandinavia.

3. The big invasions of Willow Warblers (and other species) at the Isle of May on May 5th (♀♀) and Fair Isle on 6th (♂♂) are shown to have had widely separated source-regions, and evidence is presented for the view that the Willow Warblers comprised different populations. The first represented a "maritime" (*trochilus*) group, with a south-western origin, and the second a "Continental" ("*fitis*") group, with a south-eastern source.

4. The two groups are shown to have entirely different migration timing in Europe in the spring, and it is suggested that the earlier entry of the "maritime" stock is adapted to a slower rate of advance through the coastal regions, forced upon them by the less frequent development of anticyclonic weather favourable for migration in the coastal as opposed to the Continental sector.

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