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Do willow warblers Phylloscopus trochilus of northern origin start their autumn migration at an earlier age than their southern conspecifics?

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Data on hatching time in the willow warbler for different regions (S Germany, S Sweden and N Sweden) are compared with the median of the corresponding migration diagrams. By doing so it is possible to calculate the age, at which the young of the year start their autumn migration. Our calculated values for the above mentioned regions are 68, 62–66 and 61–62 d, respectively. In our opinion this difference is too small to justify the statement, that northern birds migrate at an earlier age than their southern conspecifics. An alternative explanation is that the German migration diagrams are influenced by the passage of northern migrants, resulting in a later median and an apparently higher age for southern birds.

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Introduction

In a paper dealing with the development of plumage, body-weight and migratory restlessness in the willow warbler *Phylloscopus trochilus* L., Gwinner et al. (1972) presented results from which they concluded, that "willow warblers of the northern race *Phylloscopus trochilus acredula* start fall migration at an earlier age than conspecifics of the southern race *Ph. t. trochilus*." This statement is analysed in more detail in the present paper. Our main purpose has been to call for a general caution in the use of migration diagrams in support of different hypotheses.

Material and method

The migration of the willow warbler in southern Scandinavia is illustrated by means of migration diagrams, based on five-day-sums of birds caught at four localities: Hartsö-Enskär (58°41'N, 17°29'E), an islet in the archipelago of Stockholm, Ottenby (56°12'N, 16°24'E) at the southernmost point of Öland, and Ljunghusen (55°24'N, 12°55'E) and Falsterbo (55°23'N, 12°50'E) in southwestern Skåne.

At Ottenby all birds were caught in Heligoland traps, while in the other three places only mist-nets were used. About 50% of the birds from Ljunghusen and about 10% of the birds from Falsterbo were caught in reed-beds (*Phragmites*), while the birds in the other two cases were caught in shrubbery or gardens. The data for Hartsö-Enskär derive from Nord (1971), though corrected by us (see below), and C. Edelstam (pers. comm.) kindly supplied information for Ottenby. The figures for Ljunghusen and Falsterbo were taken from our own diaries and from the diary of Falsterbo Bird Observatory.

Information on the start of breeding in the Falsterbo area was collected by us in the years 1961–1972. A. Enemar and I. Lennerstedt kindly gave us access to 43 nest-cards from the Ammarnäs area (600 m a.s.l.), Swedish Lapland (65°58'N, 16°13'E).

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Results

Hartsö-Enskär

Fig. 1A shows five-day-sums of willow warblers caught at Hartsö-Enskär in the years 1965–1970. The figure is redrawn after Nord (1971) and the scale approximate. The total number of birds is 5540. Nord states that the median of his diagram falls on 24 August, but this can not be the case, if the diagram is correctly drawn; the correct value should be 26 or 27 August. We have chosen 26 August.

Ottenby

Referring to Hylbom (1950), Gwinner et al. (1972) have calculated the median date for the autumn migration of willow warblers at Ottenby to be 30 August. This value is based on a total of 714 birds from the years 1947–49. A close examination of the material reveals that only 73 specimens were caught in the autumn of 1947, and only 76 in 1948. The year of 1949 dominates the diagram, and the best day of this year – 30 August with 122 willow warblers caught – determines the position of the median.

Fig. 1B is based on 2842 birds caught in the years 1949–56. The median falls on 27 August. The diagram is rather flattened compared to the others, but we do not believe that more material will alter the position of the median significantly.

Ljunghusen

Fig. 1C is based on 4444 willow warblers caught in the years 1964–69. From our own experience we know, that little migration takes place before 1 August (no daily totals exceeding 20 birds in late July). Therefore this date has been chosen as start of migration. The median falls on 15 August. Twelve controls in later summers reveal, that part of the birds was of local origin. The diagram is "normal" in the sense of Berthold and Dorka (1969), but the yield in Ljunghusen has partly been dependent on the occurrence of aphids in the reed-beds, which may have influenced the position of the median (see below). Notice the small peak in September.

Falsterbo

Fig. 1D is based on 7023 willow warblers caught in the years 1964–1971, with the exception of 1967, when trapping was irregular in August. The median falls on 19 August, i.e. four days later than in Ljunghusen situated 8 km from Falsterbo. Again we notice the small peak in September.

Onset of breeding

The willow warbler begins to incubate in late May in southern Sweden; mean value for 22 clutches on the Falsterbo Peninsula is 1 June. Lennerstedt (1964) found incubation to start on 7–9 June 1963 in 12 nests in subalpine birch forest near Ammarnäs, but stated (pers. comm.), that breeding was early that year, and that it normally starts a week later. Forty-three nest-cards from the same locality, 1964–1972, gave a mean time of hatching on 29 June, equivalent to start of incubation on 16 June, provided the incubation period lasts 13 d (von Haartman 1969). The experimental birds of Gwinner et al. (1972) originated from three clutches taken near Messaure (66°42'N, 20°05'E) in 1968. They hatched on 18 June, i.e. incubation started around 5 June. Consequently mean hatching time for 58 Lapland clutches 1963–1972 was 26 June.

Summing up, the mean hatching date for southern Sweden is 14 June and for northern Sweden 26 June. The difference is 12 d, but considering the fact, that among northern willow warblers most birds breed at lower altitudes than those at Ammarnäs, the difference between South and North Swedish populations should be smaller. Kuusisto (1940) found a mean hatching date of 25 June for 8 nests in eastern Finland (lowland; 62°N, 29°E), and Slagsvold (1975), also working on

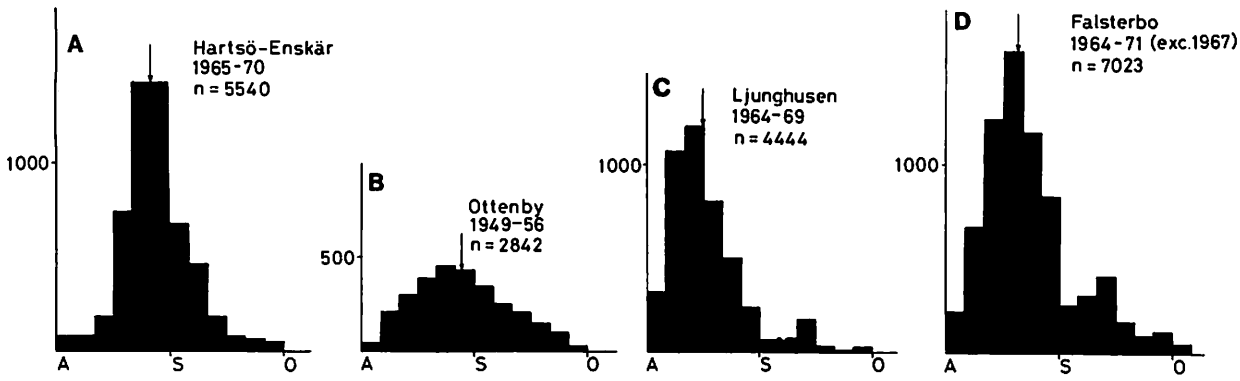

Fig. 1. Five-day means of willow warblers caught at four different localities in Sweden. Median date of migration is denoted by an arrow.

Finnish data, by three different methods concluded a delay of hatching time by 0.2, 0.5 and 0.9 days per latitudinal degree, respectively, i.e. 2–9 d between 55°N and 65°N. This is well in agreement with our own findings.

Discussion

With our paper on the migration of robins *Erithacus rubecula* at Falsterbo (Högstedt and Persson 1971) we intended among other things to give a warning against uncritical use of migration diagrams. The possibility of the occurrence of different populations with different migration patterns must always be taken into consideration.

The migration diagram from Ottenby is more suppressed and pyramidical than the three others from Sweden. The anomaly is probably due to the special facilities at Ottenby; only Heligoland traps were in use here during the fifties. In our opinion nets have a higher catching capacity than traps, a fact that was amply proven when mist-nets were introduced in Sweden. The increased capacity leads to higher numbers caught during the main period of migration; diagrams resulting from mist-net totals will therefore show a more marked character. The position of the median in such cases will also be very stable, and years of "disturbance" – with late or early migration – will not be able to dislocate it to any higher degree.

From where do the birds on the different localities originate? A few recoveries, that are considered relevant to the discussion, are listed in the Appendix. We notice that all recoveries in the breeding season of willow warblers ringed at Falsterbo and Ljunghusen in the autumn lie south of ca. 60°N, i.e. the bulk of birds passing these places in autumn belong to the South Norwegian and South Swedish populations (Fig. 2). In the case of Hartsö-Enskär we adopt the opinion of Nord (1971), that northern birds dominate here (Fig. 2). Birds ringed at Hartsö-Enskär and Ottenby have been reported from all parts of the Mediterranean area (and even in Turkey, southern USSR and Lebanon) in autumn, while 16 recoveries of birds ringed at Ljunghusen/Falsterbo show a distinct SW trend; they are all from France, Spain and Portugal. The similarity in migration routes for birds from Hartsö-Enskär and Ottenby, compared with Falsterbo and Ljunghusen, indicates that also most birds passing Otteny are of northern origin. The recovery of a willow warbler, ringed as nestling at Ammarnäs 7 July 1974, under the lighthouse "Långe Jan" at Ottenby 10 September 1974 is of special interest in this connection. If we assume an age of ten days at ringing, this bird had covered ten degrees on migration, then being 75 d of age. One bird from Västergötland was in Skåne (2 degrees) on 12 August, and was then ca 60 d old, one from Värmland in Italy (15 degrees) on 26 August, ca 70 d old.

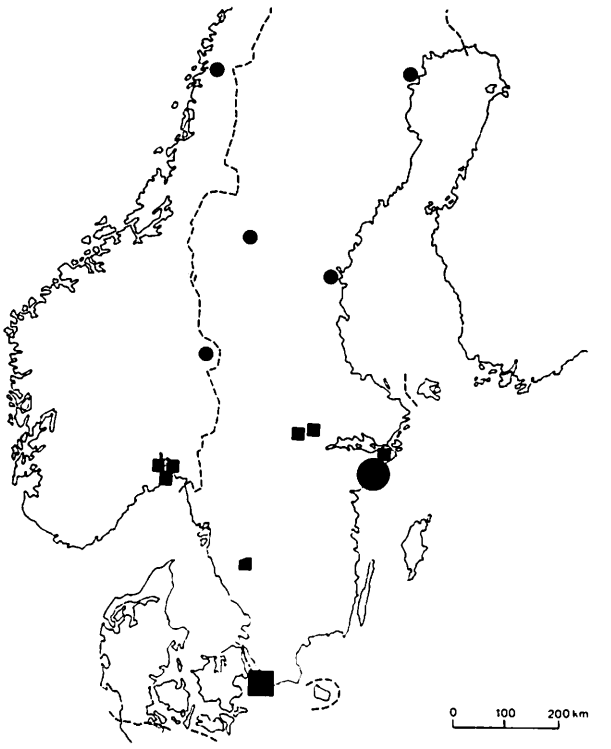

Fig. 2. Recruitment area, as shown by subsequent recoveries in June and July, of willow warblers ringed in autumn at Falsterbo (squares) and Hartsö-Enskär (circles). Large symbols denote ringing areas.

The four-day gap between the medians for Ljunghusen and Falsterbo may be a consequence of the different trapping habitats and the exploitation of aphid concentrations by willow warblers in Ljunghusen. J. Raböl, in a comment upon this paper, points out that early migration tends to be less concentrated (due to longer day, better weather etc.) to migration "bottlenecks" than migration late in the season. The median of migration diagrams from such localities will hence be retarded in time; the possibility of such an effect in the case of Falsterbo can not be excluded.

An impressive amount of recoveries of Swedish and Finnish willow warblers in the Alpine region between 26 August and 6 October support our opinion, that a "disturbance" by northern migrants occurs in the migration diagrams referred to by Gwinner et al. (1972). The poor transparency of the German paper, however, makes a comparison between our and their results difficult to perform. We believe, that their migration diagrams represent the joint migration of different populations, and not only that of a south German population. The remarkably different medians for Schwäbisch Alb (18 August), Lake of Constance (8 August) and Col de Bretolet (29 August) is probably due to the different proportions of northern migrants at the three localities. We consider 8 August to be the least

Tab. 1. Phenology of hatching and migration of willow warblers from different localities in the distribution area. The number of nests studied is given in brackets.

	S. Germany	S. Sweden	N. Sweden
Mean hatching date	1 Jun (?)	14 Jun (22)	26 Jun (58)
Median of the migration diagram	8 Aug	15–19 Aug	26–27 Aug
Mean age of the migrants (d)	68	62–66	61–62

disturbed value, the one best representing the migration of South German willow warblers. The median for Col de Bretolet, on the other hand, must be heavily biassed by the passage of Scandinavian migrants.

In Tab. 1 is shown the phenology of hatching and migration for different places. Gwinner et al. (1972) state that South German willow warblers hatch in the end of May and the beginning of June. We suppose 1 June to be the best expression for this period of time. Considering the small difference in age of the migrants and the low accuracy of some of the values, we think it unwise to state that northern willow warblers start their autumn migration at an earlier age than their southern conspecifics. An alternative explanation for the difference that occurs, when comparing migration diagrams from southern Germany with such from Sweden, could be that the former illustrate the joint migration of local and northern willow warblers. We suggest that the difference between the true value characterising a local population, and the "disturbed" value of the median, increases from north to south, or in the direction of migration.

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Appendix

A. Origin of willow warblers migrating over Skåne in autumn

1166007	.	juv	Beddinge (55.24 N/13.26 E), Skåne 24.8.63
	×		Huddinge (59.14 N/17.59 E), Sörmland 22.6.64
1261962	.	juv	Ljunghusen 16.8.65
	×		betw. Nora and Striberg (c59.32 N/15.00 E), Västmanland 11.6.66
Stat. Vilt Ås 915848	.	juv	Presterödkilen (59.16 N/10.27 E), Vestfold, NORWAY 26.8.66
	V		Falsterbo 11.9.66
Stat. Vilt Ås 916238	.	juv	Presterödkilen 30.8.66
	V		Ljunghusen 12.9.66
1280673	.	fl.	Falsterbo 11.9.65
	×		W Kåfalla (59.36 N/15.23 E), Västmanland 11.6.67
1392867	.	ad	Åhus (55.55 N/14.17 E), Skåne 21.8.68
	V		betw. Hol and Ål (60.35 N/8.25 E), Buskerud, NORWAY 7.8.71
1737870	.	juv	Smygehuk (55.20 N/13.21 E), Skåne 19.8.74
	V		Store Faerder (59.04 N/10.32 E), Vestfold, NORWAY 17.5.75
1843018	.	n.y.	Gräsåsen (57.38 N/12.33 E), Västergötland 26.6.75
	V		Löddesnäs (55.44 N/13.00 E), Skåne 12.8.75

B. Willow Warblers of Scandinavian origin in S. Germany, Switzerland and N. Italy in autumn

number?	.	?	Lilltorp (c59.04 N/17.13 E), Sörmland 29.6.41
		?	Galbiata, prov. of Como, ITALY 3.9.41
ZBG 1170	.	juv	Ledskär (60.31 N/17.43 E), Uppland 15.8.59
	+		Pumenengo (c45.40 N/9.45 E), Bergamo, ITALY 28.8.59
1022874	.	n.y.	Karlskoga (59.20 N/14.31 E), Värmland 30.6.62
	+		Castagnole Lanze (44.45 N/8.09 E), Cueno, ITALY 26.8.62
1128006	.	juv	Ottenby 7.9.62
	V		Radolfzell (47.44 N/8.59 E), Bad.-Württ., BRD 23.9.62
Helsinki *K145197*	.	ad	Valsörarna (63.25 N/21.05 E), FINLAND 22.5.62
	×		Este (45.14 N/11.38 E), Padova, ITALY 6.9.64
1015678	.	fl.	Spillersboda (59.42 N/18.51 E), Uppland 27.7.62
	(+)		Pumenengo (45.28 N/9.52 E), Bergamo, ITALY 18.9.64
1251185	.	fl.	Hartsö-Enskär 15.8.65
	(×)		Rovereto (45.53 N/11.03 E), Trento, ITALY 13.9.65

1252256	.	fl.	Hartsö-Enskär 12.9.65
	V		Moggio di Sopra (46.25 N/13.12 E), Udine, ITALY 23.9.65
1252309	.	fl.	Hartsö-Enskär 3.8.66
	+		Aviatico (45.48 N/9.47 E), Bergamo, ITALY 11.9.66
1299387	.	ad	Utklippan (55.57 N/15.42 E), Blekinge 28.5.67
	+		Vecchiano (43.47 N/10.23 E), Pisa, ITALY 17.9.67
1322346	.	fl.	Älgvikssjön (58.57 N/17.55 E), Sörmland 27.8.66
	+		Peschierea Borromea (45.26 N/9.19 E), Milano, ITALY 6.10.68
1392347	.	juv	Vittskövle (55.51 N/14.08 E), Skåne 31.7.68
	+		Romano Lombardo (45.32 N/9.45 E), Bergamo, ITALY 25.8.68
1092886	.	fl.	Getterön (57.08 N/12.13 E), Halland 28.4.68
	×		S. Eusebio (44.32 N/9.10 E), Genova, ITALY 31.8.69
1519639	.	ad	Ottenby 3.6.70
	/?/		Ponte Buggianese (43.50 N, 10.37 E), Pistoia, ITALY 10.9.70
1536914	.	n.y.	Bäckseda (57.24 N/15.05 E), Småland 21.6.71
	×		Aulendorf (47.57 N/9.40 E), Bad.-Württ., BRD 21.8.71
1542341	.	fl.	Älgvikssjön 30.8.70
	()		Bergamo (45.43 N/9.39 E), ITALY 19.9.70
1572806	.	fl.	Karlskrona (56.10 N/15.35 E), Blekinge 4.9.71
	×		Sorengo (46.00 N/8.56 E), Ticino, SWITZERLAND autumn 71
1430439	.	juv	Bälingsjön (62.00 N/17.15 E), Hälsingland 19.8.73
	/?/		Saline Joniche (38.06 N/15.39 E), Reggio di Calabria, ITALY 27.9.73
1814610	.	2k+	Ottenby 8.5.76
	/?/		Vaiano Caste del Bosco (43.40 N/10.45 E), Pisa, ITALY 29.8.76
1869758	.	2k+	Utklippan 20.5.76
	×		Riccione (43.59 N/12.39 E), Forli, ITALY 12.9.76

C. Two recoveries of willow warblers ringed as nestlings and recovered during the first and second autumn, respectively

1709761	.	n.y.	Ammarnäs 7.7.74
	×		Ottenby 10.9.74
1876081	.	n.y.	Sibbaboda (56.08 N/15.54 E), Blekinge 1.7.76
	V		Herschbach (50.34 N/7.44 E), Rh.-Pf., BRD 16.8, 17.8.77.

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