Migration routes and wintering areas of Willow Warblers *Phylloscopus trochilus* (L.) ringed in Fennoscandia

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Long distance (>400 km) ringing recoveries of Willow Warblers from Norway, Sweden and Finland were analysed. Southern Swedish and Norwegian birds migrate southwest to wintering areas around the Gulf of Guinea in Africa, whereas northern Scandinavian and Finnish populations migrate south–southeast to wintering grounds in Central, East and South Africa. Juveniles leave the natal area before adults but, due to a slow beginning, the adults pass them by the end of August. Migration seems to be faster over continental Europe, with retardation at the Mediterranean. During spring migration at least birds of northern origin seem to take a more easterly track, flying east of the Mediterranean Sea. Migration direction for juveniles showed a greater dispersion around the mean than for adults.

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Introduction

The wintering range of the Willow Warbler, *Phylloscopus trochilus*, in Africa covers the entire Afrotropical region, except deserts in the southwest and northeast (Moreau 1972). Moreau's account was based on field observations and he was unable to make any detailed conclusions about population-specific wintering areas. As ringing recoveries have accumulated, more detailed inferences have become possible. Generally, West European populations migrate southwest and East European populations southeast (Zink 1973). Finnish birds have, on average, a slightly east of south heading in the autumn (Zink 1973), and in Sweden there is a migration divide between southwest and southeast migrating populations (Hedenström & Pettersson 1984). The present paper is an attempt to further illuminate the migration directions and possible wintering areas of the Fennoscandian Willow Warblers. Data on migration timing, speed and orientation capabilities are also provided.

Material and methods

The present analysis is based on recoveries and controls of Willow Warblers ringed in Norway (138 684 ringed between 1914 and 1982, producing 115 recoveries more than 400 km from the ringing site), Sweden (324 964 ringed between 1911 and 1983, 144 recoveries) and Finland (234 539 ringed between 1914 and 1983, 98 recoveries). A further 43 recoveries of birds ringed outside the three countries but recovered there have been incorporated, giving a total of 400 for analysis. Only long distance movements were considered, thus excluding non-oriented premigratory dispersal (see Norman & Norman 1985). The limit for inclusion of a recovery in the analysis was arbitrarily chosen as 400 km minimum (great circle distance between ringing and finding sites), a distance where the bird should have done at least one night of sustained migration.

For the autumn migration, the recoveries were divided between naive (birds recovered during their first autumn migration) and experienced migrants (birds reported during autumn migration that had been ringed as adults during spring or as full-grown at least one breeding season before recovery). Centres of gravity were calculated according to formula 2 of Perdeck (1977). Great circle distance between ringing and recovery sites and angular bearing have been calculated according to standard formulas (Fredga & Fredga 1962, Kern 1962). Angular bearing from ringing to recovery site of experienced migrants are used on the assumption of resting site fi-

Table 1. Mean angular directions for Willow Warblers ringed at different latitudes. $\bar{\phi}$ is the mean angle of the sample, calculated as $\bar{\phi}$ = arc tan $(\bar{y}/\bar{x})$ if $\bar{x} > 0$ and $\bar{\phi} = 180° +$ arc tan $(\bar{y}/\bar{x})$ if $\bar{x} < 0$, where $\bar{x} = (\Sigma \cos \phi_i)/n$ and $\bar{y} = (\Sigma \sin \phi_i)/n$ (Batschelet 1981). North = 0°, east = 90°, south = 180° and west = 270°.

	All			< 58°N			58–62°N			62–66°N			>66°N		
	$\bar{\phi}$	s[a)]	n	$\bar{\phi}$	s	n	$\bar{\phi}$	s	n	$\bar{\phi}$	s	n	$\bar{\phi}$	s	n
Norway															
naive	182.5	27.6	49	–	–	–	185.2	28.9	41	169.7	13.8	8	–	–	–
experienced	193.3	25.9	29	–	–	–	200.0	17.0	23	161.6	34.1	6	–	–	–
Sweden															
naive	206.5	24.6	66	214.6	19.3	42	198.4	25.5	19	166.0	8.0	5	–	–	–
experienced	202.3	25.5	40	204.8	25.8	29	195.8	23.5	11	–	–	–	–	–	–
Finland															
naive	181.2	21.3	45	–	–	–	181.1	25.7	24	179.1	10.3	18	195.8	25.3	3
experienced	174.3	9.1	32	–	–	–	173.4	9.6	19	175.6	8.3	13	–	–	–

a) s (degrees) $= \frac{180}{\pi} (2(1-r))^{1/2}$, where $r = \frac{1}{n} ((\Sigma \cos \phi_i)^2 + (\Sigma \sin \phi_i)^2)^{1/2}$; Batchelet (1981)

delity (see Moreau 1972, Bentz 1983, Staav 1983), namely, that the same migration tracks are used in different years by individuals.

Results

Autumn migration

The mean angular migration directions and a measure of dispersion ($\bar{\phi}$ and s, see Batschelet 1981) for Willow Warblers ringed at different latitudes are summarized in Table 1. Naive Finnish birds have a mean direction near south, while experienced migrants show a slight east of south heading. The difference is, however, not statistically significant ($P>0.05$; Watson-Williams test). Swedish birds head west of south, except those ringed north of 62°N, which migrate east of south. Norwegian birds follow the same pattern, but the easternmost Norwegian long-distance recovery is from Italy (41°28'N, 12°53'E; 1964 km). The combined angular directions for Norwegian and Swedish birds ringed at southern (<62°N) versus northern (>62°N) latitudes differed significantly ($P<0.01$, Watson-Williams test). One should keep in mind, however, that full-grown birds ringed during autumn migration may originate north of the ringing site.

Recoveries of birds ringed as nestlings provide more definite information (Fig. 1; birds ringed as full-grown north of 66°N in Norway and Sweden also included). Norwegian birds migrate southwest, but recoveries of a shorter range are in a southeasterly

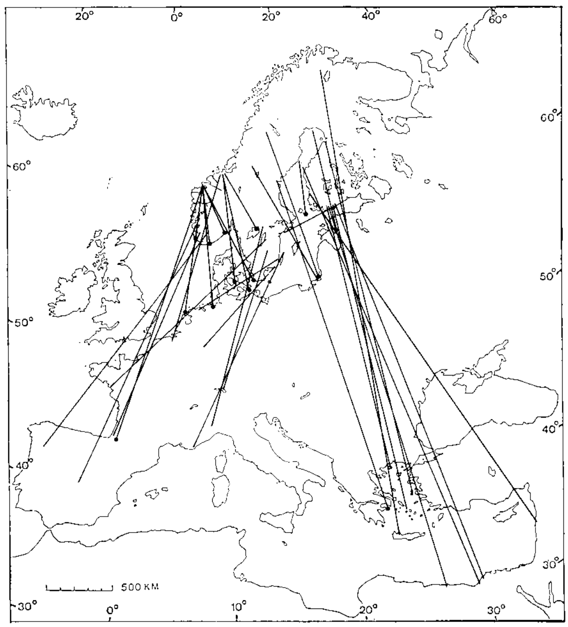

Fig. 1. Recoveries of Willow Warblers ringed as nestlings, and for Norway and Sweden also adults north of 66°N. Recoveries denoted by a dot indicate birds ringed as full-grown.

direction. Birds from southern Sweden display a southwesterly preference (the northernmost ringed at 59°20'N), whereas a bird from central Sweden (63°44'N) moved southeast. This indicates a migration divide between southwest and south–southeast

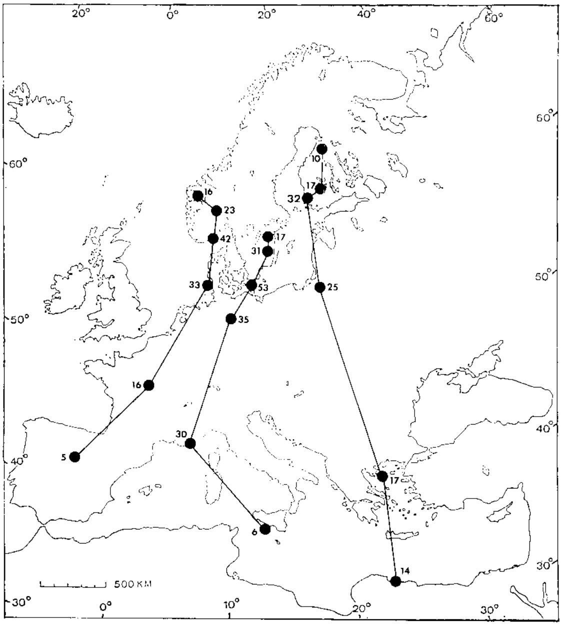

Fig. 2. Centres of gravity during half-month periods of Willow Warblers during their first autumn migration. Norwegian, Swedish and Finnish birds are shown separately. If a bird is ringed and recovered during the same period the middle point between the sites has been used. Numbers denote sample sizes. The periods are: 16–31 July, 1–15 August, 16–31 August, 1–15 September, 16–30 September and 1–15 October.

migrating contingents, somewhere between 60°N and 63°N. Among Finnish Willow Warblers a slight east of south direction is prevalent.

Seasonal timing

Centres of gravity for half-month periods of first year Willow Warblers are shown in Fig. 2. The sample sizes are greater than in Table 1 because most birds are represented by two dots (ringing and recovery sites). Swedish birds show a mean direction between Norwegian and Finnish birds, but this is partly an artefact due to the migration divide between southern and northern populations. The last Swedish point (1–15 October) shows an orientation to the southeast. This can be explained by a greater influence of northern, late migrating populations with an easterly preference. The greatest "jump" seems to be that over continental Europe, with a following retardation around the Mediterranean. Finnish birds have the fastest migration, although the latitudes for the two last periods (16–30 September and 1–15 October, respectively) do not differ between the three groups (P>0.05; pairwise Mann-Whitney U-tests).

A comparison of adult and juvenile latitudinal coordinates for September and October revealed that adults generally have migrated a bit further south, although most differences were statistically insignificant. For Finnish birds all the short range (0–400 km) recoveries were also available for analysis, and for the period 15–31 July adults are on average north of juveniles, albeit not significantly so (P>0.05; Mann-Whitney U-test). Thereafter adults are significantly south of juveniles (P<0.05) during each period.

Table 2. Average speed (km/day) of Willow Warbler autumn movements in four distance-classes. The highest speed of a single movement in each group is also shown.

Distance migrated	Average speed[a]	(n)	Maximum[b]	(days)[c]
400–1000 km	40.6	(37)	145.4	(6)
1000–2000 km	54.0	(30)	249.6	(7)
2000–3000 km	59.1	(40)	123.1	(17)
>3000 km	85.0	(22)	218.4	(47)

a) km/day
b) km/day for the bird with the highest speed
c) elapsed time in days for the bird with the highest speed

Speed of migration

The speed of migration was calculated by summing the distances covered and time intervals between ringing and recovery for categories of birds, and dividing the former sum by the latter. This method gives more weight to recoveries after a long time interval and a value closer to the real migration speed should be obtained (Hildén & Saurola 1982). The speed data are presented in Table 2, where the bird with the highest speed in every distance-class is also shown. Long distance (>3000 km) recoveries show a migration speed of 85 km/day, and those of shorter distance generally lower averages (Table 2). One bird deserves a special comment: it was ringed in Finland 14 August 1983 and found in South Africa 47 days later, resulting in an average speed of 218 km/day.

Mediterranean and African recoveries

The autumn and spring recoveries in the Mediterranean region (29–45°N) are shown in Table 3. We

Table 3. Longitudinal distribution of Willow Warbler recoveries in the Mediterranean region (29–45°N) during autumn and spring migration. The figure on the left is the number of autumn recoveries and that on the right is the number of spring recoveries.

	10°W–0°	0°–10°E	10–20°E	20–30°E	30–40°E	40–50°E	Total
Norway	25/1	3/2	2/1	–/–	–/–	–/–	30/4
Sweden	32/3	15/6	10/4	11/1	3/4	–/1	71/19
Finland	1/–	1/–	–/–	44/2	12/5	–/–	58/7

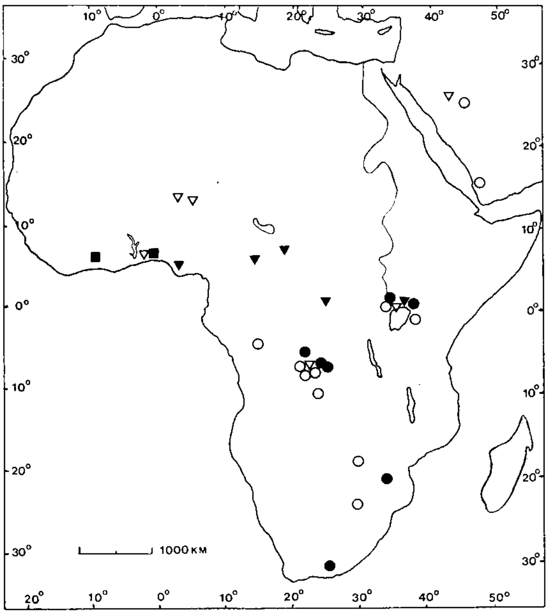

Fig. 3. Recoveries of Willow Warblers from tropical Africa and the Arabian peninsula. Filled symbols denote September–January and unfilled symbols denote February–May. Squares = Norway, triangles = Sweden and circles = Finland.

find Norwegian birds in the western part, Swedish in both the western and the eastern parts, and Finnish almost solely in the eastern part. Remarkable is the great number (29) of Finnish autumn recoveries in Egypt. For the spring recovery distribution in the Mediterranean region one notes, for Swedish and Finnish birds, a slight bias to the east compared with the autumn. Between 30–50°E there were significantly more spring recoveries than expected by chance ($P<0.05$, χ^2-test). Also within al-Maghrib, Norwegian and Swedish spring recoveries tend to be biased to the east.

All recoveries south of the Sahara and a further three from the Arabian peninsula are shown in Fig. 3. Norwegian birds are found around the Gulf of Guinea, Swedish both at the Gulf, Central and East Africa, whereas Finnish Willow Warblers are found in Central (Zaire) and East Africa (round Lake Victoria), and they are the only birds penetrating South Africa. Note the paucity of Willow Warbler records in SW Africa, as also shown by the distribution map provided by Moreau (1972). Note also that the most easterly recoveries (Arabian peninsula) are from spring migration.

Orientation

The angular distribution of ringing recoveries provides information on orientation capabilities. For Finnish-ringed birds naive migrants had a greater dispersion around the mean direction than experienced birds (Fig. 4, $P<0.02$; nonparametric test for dispersion, Batschelet 1981). The most "disoriented" bird was a juvenile recovered in Iceland. Because of the migration divide in the Norwegian and the Swedish materials (Table 1) a comparison between age classes is invalid.

Discussion

Migration directions

This study confirms the fact that there is a divide between SW and S–SE migrating populations in Sweden (Hedenström & Pettersson 1984). It is however unclear if there is an overlapping zone along the borderline, where both migration directions may occur. Why there should be such a divide remains to be resolved. A possible explanation might be that Fennoscandia has, after the last glaciation, been colonised by birds from refuges in the SW and SE, respectively. The birds from the eastern refuge have spread south in Scandinavia from Finland round the Gulf of Bothnia, until the two populations have come into contact. Migration directions have been retained. However, recent theory on evolution of migration

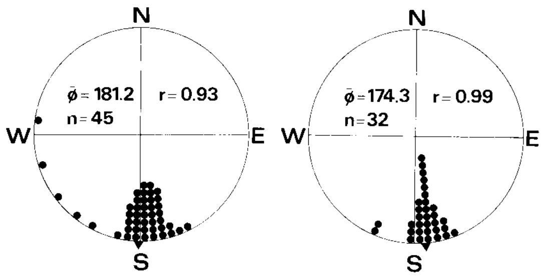

Fig. 4. Angular dispersion of (a) naive and (b) experienced Finnish Willow Warblers during autumn migration. For definitions see Table 1.

systems (Lundberg & Alerstam 1986), indicates that migration costs and asymmetric competition for early arrival in the breeding area and/or the wintering area are pivotal selective agents in the evolution of migration patterns. In the Willow Warbler, we speculate, it would be advantageous to breed in the south because of a longer favourable season with more time for replacement nesting and moult. Furthermore, to occupy these presumed favourable areas first it should be an advantage to winter as close to the breeding area as possible (West Africa). As the southern populations start the autumn migration first (Hedenström & Pettersson 1984), they can occupy the West African region before their northern conspecifics. Thus, the more northern breeding populations are displaced to wintering areas further east and south.

The mean SSE direction among Norwegian birds from 62–66°N (Table 1) results from an overrepresentation of short movements by birds trapped in Swedish observatories. At corresponding latitudes in the SW we have the North Sea where no recoveries have been reported. Perhaps most Norwegian birds follow the Swedish west-coast rather than flying directly south across the North Sea, but this is speculative. Several British passerines, including the Willow Warbler, show an initial SE migration direction followed by a change towards the SW (Evans 1966, da Prato & da Prato 1983, Norman & Norman 1985). Norwegian birds from Finnmark (northernmost Norway) migrate as Finnish birds.

Migration timing, strategy and speed

Adults were on average ahead (south) of young birds during the autumn, except for the initial stage of migration. At Ottenby (56°12'N, 16°24'E) median passing dates for adults and juveniles are 26 and 27 August respectively (years 1978–85; Ottenby Bird Observatory unpubl.). From 21 August and onwards more than 95% of young Willow Warblers have completed or are in the final stage of post-juvenile moult at Ottenby (unpubl. data from 1985 and 1986). Possibly juveniles do not reach full migration capacity until moult is finished, which is consistent with the condition for British Willow Warblers (Lawn 1984, Norman & Norman 1985). Since adults catch up with the young birds by the end of August, the migration strategy for juveniles must be an initial "hedge-hopping" until moult is completed, followed by a higher speed over continental Europe and a slight retardation at the Mediterranean Sea. The latter observation probably reflects the extra time needed to accumulate fat before crossing the Sahara.

Long-distance average speed approached 100 km/day. The five highest speeds average 196 km/day, including the extraordinary bird previously mentioned (218 km/day). One must keep in mind here that average travelling time is flight time plus the time spent resting and feeding for fat replenishment. Although some birds may move very fast over great distances, the average speed is probably close to ≈100 km/day. A bird of Willow Warbler size and weight should in still air fly at about 30 km/h (Tucker 1975), making about 300 km per night of migration. On the assumption of 300 km/night flying, an average travelling speed of about 100 km/day suggest a 3:1 relation between numbers of nights flying and numbers resting (cf. Pettersson & Hasselquist 1985). Such a relation indicates that the migration might be divided into periods of flying and resting, in agreement with the concept of "flyers" and "feeders" introduced by Rappole & Warner (1976).

Wintering area

To ring birds and wait for recoveries in tropical Africa is indeed a tiresome method to gather information on migration destinations. For example in Finland, the Nordic country with the highest number of tropical recoveries, about 16 000 Willow Warblers have to be ringed to produce one recovery south of the Sahara.

In general most Palaearctic migrants stay in the northern tropics for about 6 weeks after the Sahara crossing, then they proceed further south (Lack 1983). There is some evidence in the present study that at least a part of the Finnish Willow Warblers are an exception to this pattern — continuing directly to southern Africa. Usually, southern and western populations within Fennoscandia migrate to West Africa, whereas northern and eastern Willow Warblers fly to central, eastern and southern parts of the continent.

Spring migration

There was a tendency for recoveries made during spring migration (in the Mediterranean region) to be east of autumn recoveries. By going high (about 2000 m) and northeastwards in spring, birds crossing the Sahara have the best probability of favourable wind conditions (Moreau 1961). The spring recoveries might indicate that they do so. Autumn versus spring abundance in the eastern Mediterranean of Willow Warblers diverge from most other migrants (Moreau 1961). They are common in autumn but rare in spring, increasing in numbers in spring from the Suez Canal and eastwards. In Central Sudan they appear in large numbers in autumn, but the species is a rare spring migrant (Hogg et al. 1984). In Ethiopia it is known as a passage migrant mainly in spring (Ash 1980). The spring recoveries in Arabia and the Middle East in combination with the observational data from Sudan and Ethiopia suggest that these Willow Warblers circumnavigate the eastern Mediterranean Sea in spring.

Orientation

A greater dispersion around the mean migration direction for young birds compared with adults has also been found in, for example, the Pied Flycatcher, *Ficedula hypoleuca* (Rabøl 1978) and the Spotted Flycatcher, *Muscicapa striata* (Fransson 1986). The observed variability in the compass orientation in a population is a composite function of variation within and among individuals (Moore 1985). Using orientation cages Moore (1984) found that in naive Savannah Sparrows, *Passerculus sandwichensis*, the within-individual variability was the dominating component. Adults had significantly less within-individual variability than young migrants. If these findings apply to the Willow Warbler, the greater dispersion around the mean in young birds might be attributed to less within-individual orientation consistence, namely, they maintain a direction less accurately than adults from night-to-night. Presumably adults accomplish a greater accuracy by making use of navigational information from earlier migrations en route (Wiltschko & Wiltschko 1978). There is also a possibility that some naive birds possess a miscalibrated compass (Alerstam & Högstedt 1983) and are selected against after the first winter.

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Sammanfattning: **Flyttning och övervintringsområden för lövsångare *Phylloscopus trochilus* ringmärkta i Fennoskandien**

Långåterfynd (>400 km) av lövsångare ringmärkta i Norge, Sverige och Finland analyserades m a p flyttningsriktning och destinations-områden i Afrika. Sydsvenska och norska fåglar flyttar huvudsakligen mot SV till vinterkvarter runt Guineabukten, medan lövsångare från norra Skandinavien och Finland flyttar mot S–SO till centrala, östra och södra Afrika (Tabell 1, Fig. 1, Fig. 3). Ungfåglar lämnar häckningsområdet före de gamla fåglarna, men p g a en långsam inledningsfas av flyttningen passeras de av de adulta (2K+) fåglarna i slutet av augusti. Flyttningen tycks gå snabbare över kontinentala Europa med en retardation vid Medelhavsområdet (Fig. 2), det senare möjligen p g a extra fettpålagring inför Sahara-passagen. Under vårflyttningen tar åtminstone nordliga och finska populationer en östligare flyttningsväg (Tabell 3, Fig. 3) och passerar öster om Medelhavet. Ungfåglar uppvisade en större spridning i flyttningsriktning än äldre och därmed erfarnare fåglar under höstflyttningen (Fig. 4). Detta kan eventuellt bero på en osäkrare orienteringsförmåga hos ungfåglarna.

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