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Migration routes of North European Reed Warblers *Acrocephalus scirpaceus*

Flyttningsmönster hos nordeuropeiska rörsångare Acrocephalus scirpaceus

THORD FRANSSON & BENGT-OLOV STOLT

Abstract

Migration routes of expanding North European Reed Warbler populations were investigated by means of more than 2500 recoveries of birds ringed in Norway, Sweden and Finland. We found different autumn directions: from Norway SSW 195°–200°, from Sweden SSW–SW 211°–216°, and from Finland SW 220°–226°. Recoveries in Belgium showed that the autumn routes from the three countries passed over different areas at the latitude of Belgium. They converged at the Iberian Peninsula and continued in new directions through Morocco towards winter quarters in tropical West Africa (recoveries in Mauritania, Mali, Ghana, Ivory Coast and Liberia). In autumn, directions varied more in first-year than in older birds. In spring, the route was more direct and narrow than in autumn. Stopover in NW Africa, compared with the Iberian Peninsula, was more frequent in spring than in autumn. The SW directed routes of North European birds were similar to those of other West European populations, but differed from the SE directed autumn migration of the Hungarian, Slovakian and eastern Austrian populations.

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In Northern Europe the Reed Warbler *Acrocephalus scirpaceus* has had a long period of expansion; in Sweden since the nineteenth century (Svensson et al. 1999). The breeding range has expanded successively from a start in SW Sweden and the increasing Swedish Reed Warbler population has become the second largest in Europe after the Romanian one (Hagemeijer & Blair 1997). During the 1990s, the population was estimated at about 500,000 to 600,000 pairs (Stolt 1999). The Reed Warbler is reported to have bred in Finland only since the 1920s (Cramp 1992) and in Norway since 1947 (Haftorn 1971).

In Continental Europe there is a migration divide between Reed Warblers starting autumn migration in a south-western direction and others starting in a south-eastern direction. Those from France, Germany and Poland go south-west, while those from the Neusiedler See in Austria, from Hungary and Slovakia go south-east (Zink 1973, Schlenker 1988). Regarding North European Reed Warblers, Rendahl (1960) could report only two recoveries of Reed Warblers ringed in Sweden. Even 25 years ago, little was known about the migration routes of the North European populations. Zink (1973) did not map any recoveries of Reed Warblers ringed in Norway and Finland and only tens of birds ringed in Sweden. Dowsett et al. (1988) analysed Afrotropical recoveries and could report one Swedish recovery in each of Ivory Coast and Ghana. A south-west directed autumn migration from Sweden has successively been evident in a number of local publications (Roos 1984, Nielsen & Rönnstad 1996) and has been summed up in Cramp (1992).

The ringing of Reed Warblers increased considerably after the introduction of mist-nets during the 1950s and even more in connection with the EURING *Acro*-project (cf. Jenni et al. 1994) in the 1980s. As a result of the increase in ringing there has been a large number of recoveries. Actually, many of the recoveries are caused by ringing activity and are controls made by other ringers far from the ringing sites. In this study, we analyse the recoveries of Reed Warblers ringed in Norway, Sweden and Finland regarding directions of autumn migration and routes through Europe.

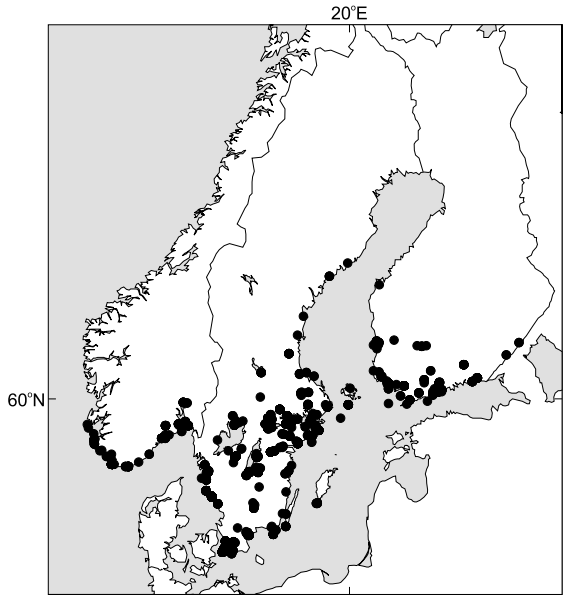

Figure 1. Ringing sites for Reed Warblers *Acrocephalus scirpaceus* recovered up to and including 1998 at a distance of more than 10 km.
Märkplatser för rörsångare Acrocephalus scirpaceus *som återfunnits mer än 10 km från märkplatsen t.o.m. 1998.*

Material and methods

The number of Reed Warblers ringed up to and including 1997 was about 17,500 in Norway, about 290,000 in Sweden and about 37,000 in Finland. The ringing sites for birds that were later recovered are mainly situated in the southern parts of the countries (Figure 1). The number of recoveries of birds found more than 10 km from the ringing site up to and including 1998 totals 2567, of which 186 (7%) were birds ringed in Norway, 1966 (77%) in Sweden and 415 (16%) in Finland. The number of foreign recoveries is 113 from Norway, 1129 from Sweden and 192 from Finland. About 31% of autumn recoveries are from birds controlled alive in Belgium. This is largely due to the use of mistnets in combination with playback of song in order to attract migrants by many ringing groups in Belgium.

From the three Nordic countries, the mean directions of orientation during autumn migration were calculated according to the loxodrome, which is the route between two points that follows a constant compass bearing. This was done for two sets of recoveries. The first set includes all recoveries during July–November in the same year as ringing and within the range 400–4500 km from the site of ringing. This range covers approximately an area southward to and including Morocco. The second set consisted of all recoveries during July–November made south of latitude 49° N, which means south of Belgium, and a distance from ringing in most cases within the range 1200–4500 km. The proportions of ringed birds that are controlled in Belgium, from the different countries, are calculated and compared as they may indicate differences regarding the geographic area passed during autumn migration.

Results

Direction of autumn migration

The autumn migration is directed mainly SSW–SW (Figure 2). Autumn directions are SSW 195° (n=60) from Norway, SW 216° (n=669) from Sweden and SW 226° (n=110) from Finland, calculated on recoveries in the same year as ringing and within the range 400–4500 km from the ringing site. The mean directions (loxodrome) of birds leaving the breeding areas in Norway and Finland are significantly different from the mean direction of birds leaving Sweden (Watson-Williams test: $F=207.9$, $p<0.001$ and $F=60.5$, $p<0.001$, respectively).

Directions calculated only from recoveries made south of 49° N, which means south of Belgium, are SSW 200° (n=5) from Norway, SSW 211° (n=173) from Sweden and SW 220° (n=24) from Finland. These directions differ by 5–6° from the ones calculated on the first set of recoveries. This is a result of the large number of birds controlled in Belgium, affecting the calculations based on all recoveries. The difference between areas of origin is, however, consistent and the mean directions of birds from Norway and Finland are significantly different from the mean direction of birds from Sweden (Watson-Williams test: $F=10.3$, $p<0.01$ and $F=32.9$, $p<0.001$, respectively). The proportions of ringed birds controlled in Belgium are significantly different between the three countries, as shown by 95% confidence limits (Table 1).

Age specific differences in orientation of autumn migration

For birds from Sweden, we found a larger variation of direction in first year birds than in second year and older birds (Figure 3; nonparametric test for dispersion, $z=4.82$, $p<0.001$, Batschelet 1981). Second year and older birds follow a narrower and

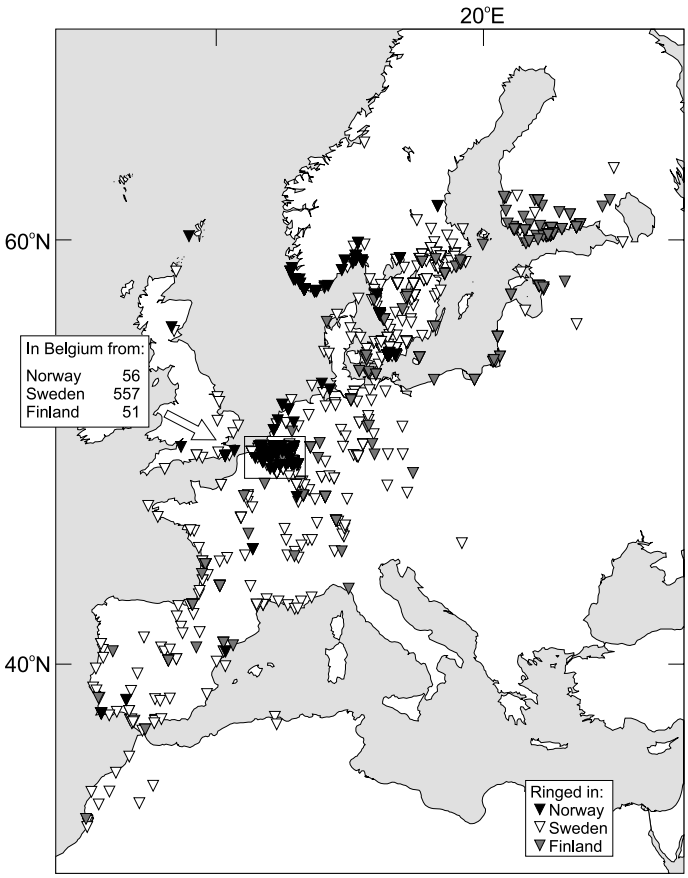

Figure 2. Recoveries during July–November up to and including 1998 of Reed Warblers *Acrocephalus scirpaceus* ringed in Norway (n = 159), Sweden (n = 1625) and Finland (n = 342). All recoveries at a distance of more than 10 km are included.
Återfynd under perioden juli–november t.o.m. 1998 av rörsångare Acrocephalus scirpaceus *ringmärkta i Norge (n=159), Sverige (n=1625) och Finland (n=342). Alla fynd med avstånd större än 10 km är inkluderade.*

Table 1. Reed Warblers Acrocephalus scirpaceus controlled alive in Belgium in relation to numbers ringed in Norway, Sweden and Finland.
Rörsångare Acrocephalus scirpaceus *kontrollerade av ringmärkare i Belgien i relation till antalet märkta i Norge, Sverige och Finland.*

Country *Land*	Number ringed *Antal märkta*	Controlled in Belgium number *Kontrollerade i Belgien antal*	% *%*	95% conf. Interval *95% konfidensintervall*
Norway *Norge*	10 509	54	0.514	0.377–0.651
Sweden *Sverige*	133 830	462	0.345	0.314–0.376
Finland *Finland*	19 580	40	0.204	0.141–0.267

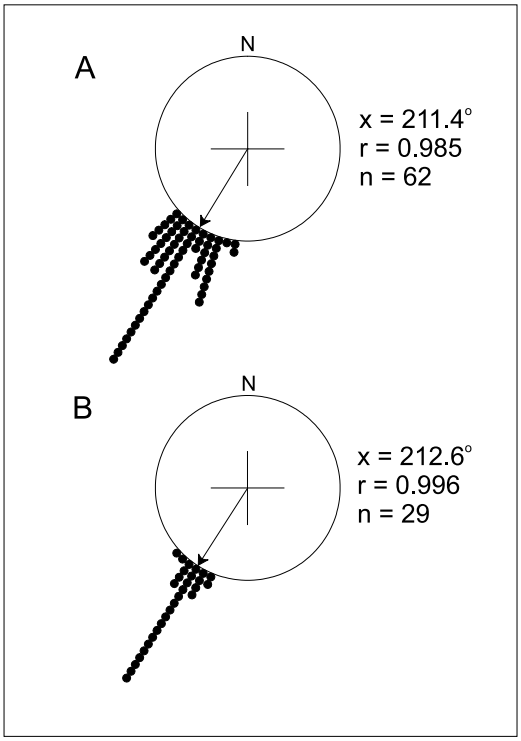

Figure 3. Direction of autumn migration (July–November) of first-year (A) and older (B) Reed Warblers *Acrocephalus scirpaceus* ringed in Sweden based on recoveries others than controls made by ringers. Recoveries of birds found in Norway, Denmark, Sweden, Finland and the Baltic States are not included. The reason for excluding recoveries from this area is that birds ringed in one year and recovered as adults north of the ringing site in another year are not relevant to the calculation. There are no recoveries in Finland and the Baltic States of first year birds ringed in Sweden.
Riktning för höstflyttning (juli–november) hos unga (A) och gamla (B) rörsångare Acrocephalus scirpaceus *ringmärkta i Sverige baserat på återfynd som inte är kontroller av ringmärkare. Återfynd av fåglar i Norge, Danmark, Sverige, Finland och de Baltiska länderna är inte inkluderade. Skälet till detta är att fynd från områden norr om märkplatsen av gamla fåglar ett senare år inte är relevanta för beräkningen. Det finns inga återfynd i Finland eller de Baltiska länderna av ungfåglar märkta i Sverige.*

more concentrated route than first year birds do, which is obvious from the geographical distribution of the recoveries (Figure 4).

Wintering area

Inland recoveries in tropical West Africa (Mauritania, Mali, Ghana, Ivory Coast and Liberia) of birds ringed in Sweden indicate where the main wintering area of birds from breeding areas in northern Europe is situated (Figure 5). Recoveries south of the Sahara of Reed Warblers ringed in Norway and Finland are still (beginning of 2005) lacking. It is obvious that the Reed Warblers have to continue in new directions when they have left Europe in order to reach winter quarters in tropical West Africa.

Route of spring migration

In principle, the spring migration follows the same routes as the autumn migration, although in spring, recoveries are lacking along the European Atlantic coast from Portugal to England and also from the Central and Eastern parts of Continental Europe (Figure 5). This points to a more direct, narrower and more concentrated route in spring than in autumn. The distribution of recoveries within North Africa and Southwest Europe (the Iberian Peninsula) is not the same in spring as in autumn. A larger proportion of the recoveries is found in North Africa in spring (χ^2=16.6, df=1, $p < 0.001$).

Discussion

Available data on the northward expansion in range of the Reed Warbler points to a successive immigration into Finland and Norway from SW Sweden during the 20th century (cf. Svensson et al. 1999). We found differences in mean directions, which indicates that, during the same period, there has evidently been a differentiation in the mean autumn direction of orientation between populations leaving their different new breeding areas in autumn. It has earlier been shown that changes in direction of migration can take place over a relatively short period of time, which has been observed especially from studies of the Blackcap *Sylvia atricapilla* (Berthold & Helbig 1992, Berthold et al. 1992). We found in the Reed Warbler a larger scatter of directions in first year birds than in older birds. This is the case also in many other bird species (cf. Alerstam 1990). The lesser scatter of directions in older, experienced birds may be an effect not only of experience, but also a result of selection in favour of individuals starting migration from the specific breeding area in the most optimal direction.

From ringing recoveries of passerine birds breeding in Northern Europe and wintering south of the Sahara it is known that a number of dif-

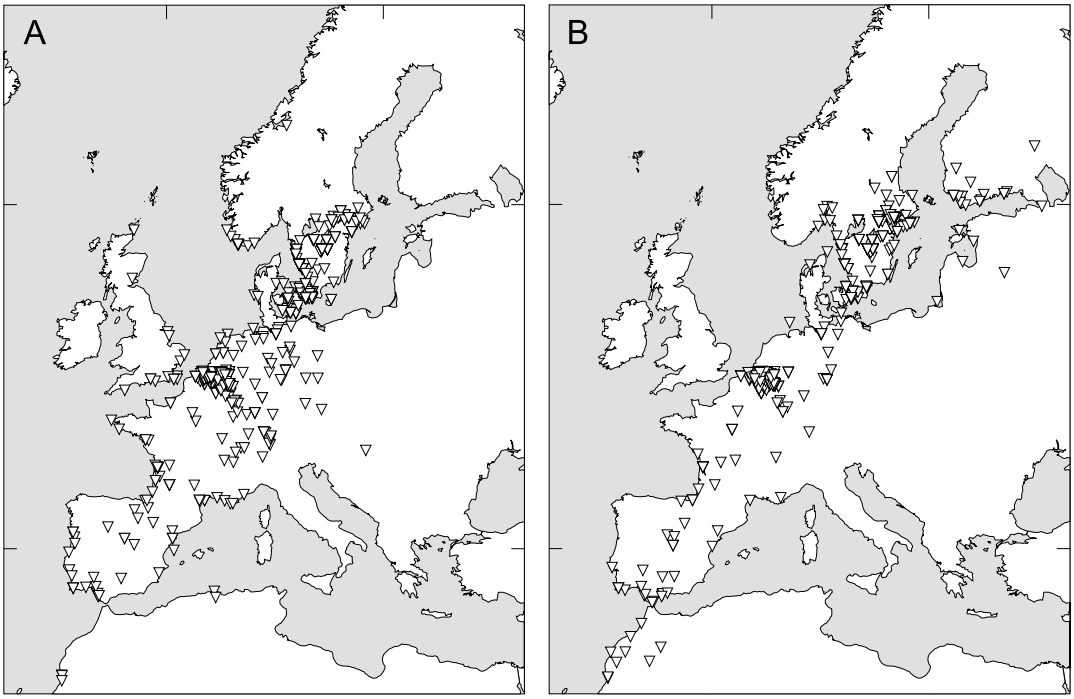

Figure 4. Autumn recoveries (July–November) of Reed Warblers *Acrocephalus scirpaceus* ringed in Sweden separated on (A) first year birds (n=916) and (B) second year and older birds (n=681). The recoveries in Finland and other countries east of the Baltic (B) may be from birds of other than Swedish origin but ringed when passing Sweden on migration in earlier years.

Höstfynd (juli–november) av rörsångare Acrocephalus scirpaceus *ringmärkta i Sverige, uppdelat på (A) unga (n=916) och (B) gamla (n=681) fåglar. Återfynden i Finland och andra länder öster om Östersjön kan vara av fåglar med ursprung utanför Sverige, men märkta i Sverige under flyttning ett tidigare år.*

ferent migratory patterns are realised (e.g. Zink 1973, 1975, Stolt 1977, Fransson 1986). The main differences are between species or populations following a western, a central or an eastern route when passing the Mediterranean Sea. The North European Reed Warblers belong to those following the western route. From the Nordic countries, their routes through Central Europe pass over different areas but converge in the eastern part of the Iberian Peninsula (Figure 6). This is in contrast to some other species, where migration routes of different populations run parallel to each other through Europe. For instance, in Sedge Warbler *Acrocephalus schoenobaenus* and in Garden Warbler *Sylvia borin*, Finnish populations pass the Mediterranean further to the east than Scandinavian populations do (e.g. Zink 1973). It is also in contrast to the Pied Flycatcher *Ficedula hypoleuca*, which is found in the absolute western part of the Iberian Peninsula (Zink 1975). It is interesting to note that in the recently established Reed Warbler populations in Norway and Finland, it is the direction of orientation at the start of autumn migration that has been changed, while the area for the passage of the Iberian Peninsula, has remained unchanged. For the Reed Warbler, as well as for many other migrating species, there may be an advantage to prepare for the Saharan crossing on the Iberian Peninsula or in Northwest Africa, and it is also obvious that the distribution of land facilitate passage to occur in this area. However, converging routes within species have also been found in the eastern Mediterranean area, resulting in more or less species-specific recovery areas during autumn migration (Fransson et al. 2005).

The SSW–SW directed routes through Europe, as well as recoveries south of the Sahara of birds ringed in Sweden, point to winter quarters in-

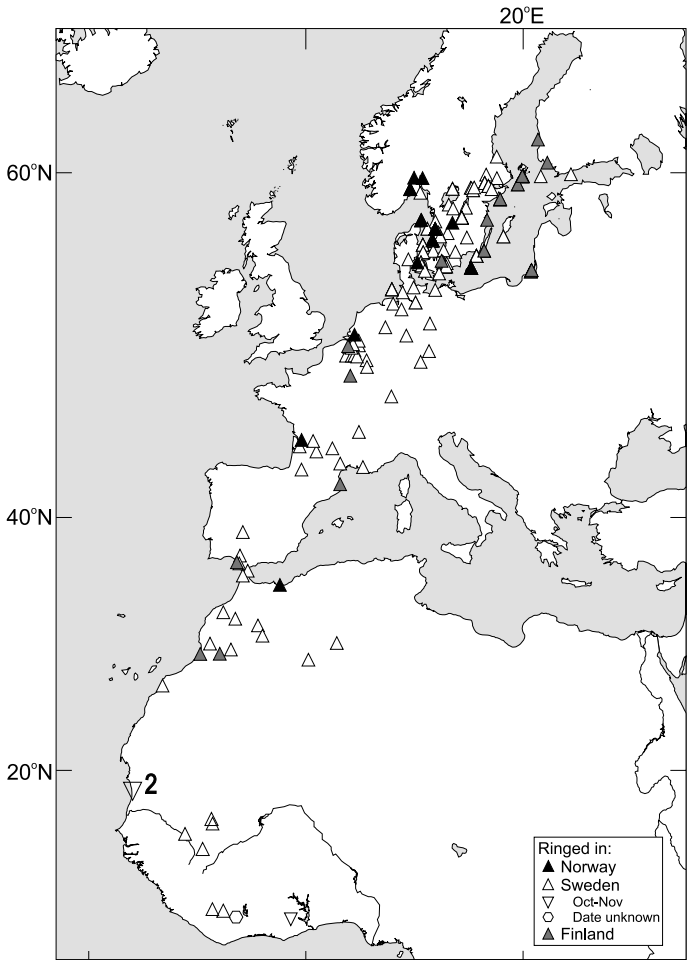

Figure 5. Recoveries during March–May up to and including 1998 of Reed Warblers *Acrocephalus scirpaceus* ringed in Norway (n = 16), Sweden (n = 176) and Finland (n = 26). Recoveries at a distance of more than 10 km are included. In addition, four recoveries from tropical West Africa, three from the autumn and one with date unknown. The recoveries in tropical West Africa have been updated and include all recoveries received up to and including 2004.
Återfynd under perioden mars–maj t o m 1998 av rörsångare Acrocephalus scirpaceus *ringmärkta i Norge (n=16), Sverige (n=176) och Finland (n=26). Alla fynd med avstånd större än 10 km är inkluderade. I tillägg har fyra fynd från tropiska Västafrika inkluderats, tre från hösten och ett med fynddatum okänt. Fynden i Västafrika har uppdaterats och gäller samtliga fynd erhållna t.o.m. 2004.*

land in tropical West Africa. This is largely the same wintering area as indicated by Dowsett et al. (1988) for other West European populations, even if recoveries from Britain & Ireland mainly are found more to the west, close to the coast in West Africa (Wernham et al. 2002). For the Reed Warblers from the Nordic countries, as for many other migrants using this route, a change of the mean direction of orientation takes place after they have left Europe. Such a detour can, by a shorter barrier crossing, decrease the overall transport cost (Alerstam 2001). The change in migratory direction has been shown to occur in Garden Warblers held under experimental conditions, indicating that it is controlled by the endogenous rhythm (Gwinner & Wiltschko 1978). However, the present recoveries along the route through West Africa are too few to allow any hints about where this change occurs and to what degree it is influenced by leading lines of the landscape. During spring migration, a larger proportion of the recoveries than in autumn is found in North Africa compared with the Iberian Peninsula. This indicates that Reed Warblers use North Africa for stopover more frequently in spring than in autumn. This seems to be a common pattern for several long-distance migrating North European passerines (cf. Zink 1973, 1975).

For West and Central European populations of the Reed Warbler, a SW directed autumn migration towards the Iberian Peninsula was shown by Zink (1973) and described in Cramp (1992). We can conclude that the relatively recently estab-

lished northern populations also follow this migratory pattern. This is different from the SE-migrating Reed Warblers from eastern Austria, Hungary and Slovakia reported by Schlenker (1988).

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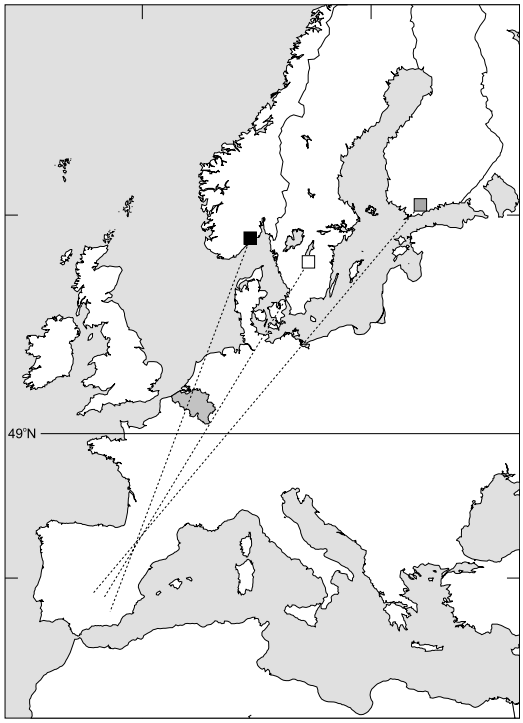

Figure 6. Mean autumn directions (broken lines) of Norwegian, Swedish and Finnish Reed Warbler *Acrocephalus scirpaceus* populations calculated for birds recovered south of 49°N. The three directions are extended as broken lines from the mean positions for the ringing sites in the different countries. The directions are from Norway SSW 200°(n=5), from Sweden SSW-SW 211°(n=173), from Finland SW 220°(n=24).
Genomsnittliga flyttningsriktningar under hösten (streckad linje) för rörsångare Acrocephalus scirpaceus *ringmärkta i Norge, Sverige och Finland, beräknade utifrån återfynd söder om 49°N. De tre riktningarna utgår från den genomsnittliga märkplatsen i de olika länderna. Riktningen är från Norge SSW 200° (n=5), från Sverige SSW-SW 211°(n=173) och från Finland SW 220° (n=24).*

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Sammanfattning

Rörsångaren *Acrocephalus scirpaceus* har expanderat sitt utbredningsområde norrut i Europa under lång tid. I Sverige sedan 1800-talet medan arten började häcka i Finland först på 1920-talet och i Norge sedan 1947. På kontinenten är det känt att arten har en sträckdelare och fåglar från Frankrike, Tyskland och Polen flyttar mot sydväst medan fåglar från Österrike, Ungern och Slovakien flyttar mot sydost. Kunskapen om de nordeuropeiska rösångar-populationernas flyttningsmönster var länge begränsad, men under senare tid har det framkommit att de har en sydvästlig flyttningsriktning. Märkningen av rörsångare ökade kraftigt efter det att slöjnäten introducerades på 1950-talet och även mer när Acro-projektetet startades av EURING (European Union for Bird Ringing) under 1980-talet. Den ökade märkningen har också resulterat i ett ökat antal återfynd, varav många gäller kontroller av ringmärkare långt från märkplatsen. I denna artikel analyseras återfynd av rörsångare märkta i Norge, Sverige och Finland (Figur 1) med avseende på flyttningsvägar och flyttningsriktning.

Flyttningen under hösten är huvudsakligen riktad mot SSW-SW (Figur 2). Fåglar märkta i Norge flyttar i genomsnitt mot SSW (195º, n=60) medan fåglar märkta i Sverige flyttar mot SW (216º, n=669) liksom fåglar märkta i Finland (226º, n=110). Den genomsnittliga riktningen för fåglar märkta i Sverige är signifikant skild från fåglar märkta i Norge (Watson-Williams test: F=207,9, p<0,001) och Finland (F=60,5, p<0,001). Beräknas flyttningsriktningen enbart med utgångspunkt från fynd söder om 49ºN erhålls något annorlunda riktningar (Norge 200º, Sverige 211º and Finland 220º), men skillnaden mellan länderna består. Detta beror på att ett stort antal fåglar kontrollerats i Belgien (som ligger norr om 49ºN) och att detta påverkar beräkningarna. Den andel av de märkta rörsångarna som kontrolleras i Belgien skiljer sig åt för de olika länderna (Tabell 1), vilket styrker att de olika populationerna har skilda flyttningsvägar när de passerar Belgien. Rörsångare märkta i Sverige och återfunna under sin första höstflyttning uppvisar en större variation i flyttningsriktning jämfört med höstfynd av gamla fåglar (Figur 3). Att äldre fåglar följer en smalare och mer koncentrerad flyttningsväg är också tydligt från den geografiska fördelningen av återfynd under höstflyttningen (Figur 4). Fynden från våren visar att fåglarna i stort sett följer samma flyttningsväg som under hösten. Färre fynd längs Atlantkusten samt i den östra delen av kontinentala Europa antyder dock att de under våren följer en mer direkt och smalare flyttningsväg (Figur 5). En större andel av fynden under våren har, jämfört med hösten, rapporterats i Nordafrika i stället för på den Iberiska halvön. Detta är ett vanligt mönster bland tropikflyttare och förmodligen ett resultat av att Nordafrika, där nederbörd faller under vintern, är lämpligare som rastningsområde under våren än under hösten. Fynd i inlandet i tropiska Västafrika av rörsångare märkta i Sverige antyder var övervintringsområdet för de nordeuropeiska populationerna är beläget (Figur 5). Fortfarande (början av 2005) saknas tropikfynd från Norge och Finland så det är okänt om de nordliga populationerna övervintrar i samma område. För att nå övervintringsområdet måste fåglarna ändra flyttningsriktning i södra Europa eller i Nordafrika. Rörsångare märkta i Storbritannien har främst rapporterats i kustnära områden i Västafrika, tydligt väster om de svenska inlandsfynden.

Resultaten från denna studie visar att de relativt nyetablerade populationerna av rörsångare i norra Europa skiljer sig åt när det gäller flyttningsriktning, men att de tycks ha bibehållit ett gemensamt område som de passerar den Iberiska halvön och Nordafrika (Figur 6). Att rörsångarna koncentreras på detta sätt kan bero på att de behöver utnyttja områden på den Iberiska halvön eller i Nordvästra Afrika inför passagen av Sahara. Det kan naturligtvis också bero på de geografiska förhållandena, men populationer av en del andra arter i norra Europa, t ex sävsångare och trädgårdssångare, passerar Medelhavet på bred front, medan t ex svartvit flugsnappare är starkt koncentrerad till den västra delen av den Iberiska halvön. I östra Medelhavet, i nära anslutning till passagen av Sahara, har det nyligen visats att flera arter under hösten uppträder mer eller mindre artspecifika områden.