

The Migration of the European Redshanks **(*Tringa totanus* (L.)).**

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(Med et dansk resumé: De europæiske Rødbens (*Tringa totanus* (L.))
trækforhold.)

The movements of the Redshank are rather well-known in Europe, where this species almost everywhere is a quite common bird. Recent ringing in Scandinavia, however, has revealed some new and interesting facts. The conclusions drawn in this paper are mainly based on the considerable number of recoveries of Scandinavian Redshanks. There are no less than 154 recoveries abroad of Redshanks ringed in Denmark. The corresponding figures for Sweden and Norway are 53 and 8, respectively. In most other countries ringing of Redshank has been carried out on a modest scale only.

I am indebted to Dr. HANS JOHANSEN, Zool. Museum, Copenhagen, for giving me access to the ringing records of the Danish Redshanks not yet published, and to Dr. G. C. A. JUNGE, Rijksmuseum van Natuurlijke Historie, Leiden, to Prof. Dr. R. DROST, Vogelwarte Helgoland, Wilhelmshaven, and to Dr. H. HOLGERSEN, Stavanger Museum for various information about recoveries of Dutch, German and Norwegian Redshanks, respectively. I also wish to thank Mr. ERIK PETERSEN for carefully drawing the maps in this paper.

The Danish Population.

The Danish breeding stock leaves the country very early in the autumn, the adult as a rule in the latter half of July, the young birds usually not until August. Redshanks can be seen in small numbers until mid-September, but these birds are probably passage-migrants, coming from further north. Later in the autumn Redshanks are only exceptionally met with in Denmark, apart from Iceland birds (cf. below, p. 111).

A part of the Danish Redshanks, recovered abroad, have been ringed as nestlings, but by far the greater number were ringed as juveniles or adults, being caught in traps. Due to the activity of Messrs MARDAL JENSEN and P. THOLSTRUP a

TABLE I. Recoveries of Redshanks (*Tringa totanus*) Ringed in Denmark, arranged according to Localities and Month of Recovery.

Genfangster af Rødben (Tringa totanus), ringmærkede i Danmark, opstillet efter lokalitet og måned for genfangsten.

Locality	Autumn-passage Efterårstræk			Wintering Overvintrende					Spring-passage Forårstræk			Summe- ring Oversom- rende		Total Ialt
	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	
Veneto	8	4	5	1	..	2	..	4	1	25
NW. Italy	2	3	1	6
S. Italy	1	..	2	..	1	4
Sicily	1	1
Sardinia	2	..	1	1	4
Holland	1	1
Belgium	1	1	2
N. France	2	..	1	1	2	6
W. France	1	9	1	1	3	1	2	..	1	3	22
S. France	2	13	5	4	3	4	6	2	2	..	1	1	..	43
Interior France	1	1	2
Portugal	1	5	1	3	1	2	..	1	14
SW. Spain	1	2	..	3	1	..	1	1	1	10
E. Spain	1	3	1	1	3	9
Interior Spain	1	1
England	1	1
Tunisia	1	1
Morocco	1	1	2
Total (Ialt) ...	4	37	21	13	22	9	16	9	10	8	3	1	1	154

number of traps have been in operation on the coasts of the island of Amager, near Copenhagen, and a very large number of shore-birds have been ringed there in recent years. The majority of the Redshanks caught in traps on Amager are no doubt stragglers or passage-migrants from Zealand and Scania, and possibly from the Kattegat coasts of Halland and Bohuslän, but as the two groups mentioned (the birds ringed as nestlings and those ringed as grown-up juvenile or adult birds) show no differences in their movements they have been united in this study. Of the 154 recoveries abroad of ringed Danish Redshanks 44 only have been published (cf. DONARK 1953, p. 251, where references are given to all recoveries published). The remaining 110 recoveries originate from 1951–53 (actually to Feb. 1954), for which years the annual lists of recoveries have not yet been published.

It would require too much space to enumerate the individual recoveries, but all recoveries of Danish Redshanks are listed

in table I, arranged according to locality and month of recovery. The recoveries have been divided into four groups, *viz* birds recorded on autumn-passage, wintering, on spring-passage and summering. Birds recorded abroad in the period from mid-July to the end of September have been presumed to be on passage. This does not imply that they may not have reached the winter-quarter in this period, but it means that we cannot be sure that they are not on passage until October. On the other hand, we can safely deduce that recoveries made after 1st October belong to wintering, not to migrating birds, apart from mere exceptions. The breeding-birds return to Denmark in mid-March and onwards. Therefore, birds recovered from 1st March to early May are presumably on spring-passage, although naturally some may stay in the winter-quarters after 1st March. Finally, specimens recovered abroad in June or early July in years subsequent to the ringing year have been regarded as summering birds, *i. e.* they have remained far south of their breeding-area, probably owing to disturbances in the hormonal balance controlling the vernal recrudescence of the gonads.

All recoveries are listed on the map fig. 1 and arranged in table I in a number of groups in accordance with the migration routes and the winter-quarters. The situation of each group of recoveries will be briefly dealt with below:

Veneto. This area covers NE. Italy and not only includes the province of Veneto but extends southwards to Ravenna and even includes a single record from Romagna. Eastwards the area extends to the Triest boundary and includes a single record from Rovigno. Material: Venezia-Veneto (19 recoveries), Comacchio (1), Ravenna (2), Gorizia (1), Rovigno (1), Romagna (1). This area is an important wintering-place for the Danish Redshanks. The winter-records (8), however, constitute only 67 % of the autumn-migrants (12), which shows that a number of birds continues the migration further south.

NW. Italy. Material: Piemont (1 recovery), Genova (1), Toscana (3), Roma (1). This area is unimportant as a winter-quarter for the Danish Redshanks, all 6 recoveries being from the migration time.

S. Italy. Material: Brindisi (1 recovery), Foggia (1), Taranto, Puglia (1), Reggio di Calabria (1). The fact that 3 of these 4 recoveries are winter-records indicates that the migration rarely surpasses this area.

Sicily. One recovery: Augusta, 13th April (spring-passage).

Sardinia. Four recoveries, 3 of which from Cagliari, 1 from "Sardinia", all being winter-records. This indicates that the migrants arrive rather late and usually do not continue further south.

Holland. One recovery: Petten, 29th January 1954.

Belgium. Two recoveries: Dixmuyde 24th July and Antwerp 28th April.

N. France. This area covers the coast from the Belgian border to Bretagne. Material: Dept. Somme (3), dept. Seine Inférieure (1), Baie de Seine (1), dept. Calvados (1).

W. France. This area covers the coast of the départements Vendée, Charente Inférieure, Gironde and Landes. Material: Aiguillon, dept. Vendée (1), dept. Charente Inférieure (6), dept. Gironde (13), dept. Landes (2). The number of winter-records (7) constitutes only 64 % of the autumn-records (11), which shows that part of the migrants continues farther south. This is borne out also by the dates of the wintering birds. The single Vendée recovery (from Aiguillon, which is situated in the southernmost part of Vendée) is from September, the 5 Charente-Gironde winter-recoveries are from October-December, and the two Landes recoveries are both from January. This indicates that the migrants move slowly to the south during winter.

S. France. This area covers the départements Bouches-du-Rhône, Hérault, Gard, Aude and Pyrenées-Orientales. There are no less than 43 recoveries, the greater part from the extensive lagoons and estuaries of dept. Bouches-du-Rhône (La Camargue) and Hérault, which constitute by far the most important winter-quarter of the Danish Redshanks. Material: Bouches-du-Rhône (21), Hérault (18), Aude (2), Gard (1), Pyrenées-Orientales (1). The number of winter-records (19) practically equals that of the autumn-migrants (20), indicating that a small number only continues further on the migration. A single record (from Hérault) given as "winter" has been placed among the January-recoveries. The latest spring-record is from 3rd May (from Hérault), but there is also a June-recovery (also from Hérault), which has been assumed to be a summering bird.

Interior France. A record from Thiers (August) and one from dept. Cantal (March) evidence that migration takes place across the continent and not only along the coasts.

Portugal. Material: Porto (1), Aveiro (3), Figueira-da-Foz (2), Savavem, near Lisbon (2), Setubal (2), Faro (2), Castro Marim (2). All localities are situated along the coast. The number of winter-records (7) slightly exceeds that of the autumn-records (6), showing that only a small number of birds continues further south. A recovery from Sacavem, given as "winter", has been incorporated in the January-records.

SW. Spain. This area covers the coast from the Portuguese border to Malaga. Material: Delta of river Guadalquivir (1), Las Marismas of San Fernando (2), Cadiz (4), Malaga (3). Just as in Portugal the number of winter-records (5) exceeds that of the autumn-records (3).

E. Spain. This area covers the east coast of Spain from the French border to Torrevieja (38° n. lat.). Material: Tarragona (3), delta of river Ebro (1), Valencia (2), Alicante (2), Torrevieja (1). All recoveries from this area are from the winter-time, which shows that the Danish Redshanks usually do not continue further south on their migration.

Interior Spain. A summering bird, recovered on 2nd July at the river Huebra, in the province Salamanca. This recovery has not been plotted on the map fig. 1, which shows the passage-migrants and the winter-visitors, not the summering birds.

England. Only one record: Mersey Island (in the estuary of the river Colne), 9th Febr. 1952.

N. Africa: There are 3 recoveries, all from winter, *viz*: Bizerte, Tunisia (1), Rabat, Morocco (1), Mazagan, Morocco (1).

The autumn-migration of the Danish Redshanks takes place very rapidly, no doubt often in one stretch from Denmark to the winter-quarter. The arrival there (in France and northern Italy) takes place usually in Aug., but there are some extremely early recoveries, which show that the winter-quarter is sometimes reached as early as July. Four July recoveries: Dixmuyde, Belgium, 24. July (passage-migrant); dept. Gironde, W. France, 29. July; dept. Hérault, S. France, 28. July; and dept. Hérault, S. France, "end July". The arrival in more southern areas (S. Italy, Portugal, Spain) takes place usually in Sept.; recoveries in Aug. are rare, and there are no July recoveries at all. The difference in time of arrival between the more "northern" winter-grounds and the more southern ones appears from the following table:

Number of monthly recoveries of autumn-migrants (in %):

Northern:	July	Aug.	Sept.	Number
Veneto, Italy	0	67	33	12
W. France	9	82	9	11
S. France	10	65	25	20
Southern:				
Portugal	0	17	83	6
SW. Spain	0	33	67	3

The recoveries show that there is more than one migration route or direction. One part of the Danish population moves along the European sea-coasts, passing Holland and France and continuing to Spain and Portugal. Another part moves across the inland, heading directly for the Mediterranean coast



Fig. 1. Recoveries of Redshanks (*Tringa totanus*) ringed in Denmark. Solid circles: Recoveries in winter (Oct.-Feb.). Open circles: Recoveries in migration time (July-Sept. & March-May). Figures: Number of recoveries.

Genfangster af Rødben (*Tringa totanus*) ringmærkede i Danmark. Udfyldte cirkler: Genfangster om vinteren (okt.-febr.). Åbne cirkler: Genfangster i træktiderne (juli-sept. & marts-maj). Tallene angiver antal genfangster.

of France and the Adriatic coast of Italy. The distinction between a coastal (Atlantic) migration route, heading towards SW., and an interior (continental) route, heading almost due S., is found among a number of Danish birds, according to the results of ringing. Among the waders this is most pronounced in the Redshank, the Ruff (*Philomachus pugnax*) and the Wood-Sandpiper (*Tringa glareola*). The Redshank is known to be a regular passage-migrant in Germany, Switzerland and France, but evidently it hastens through these countries and probably sometimes even will carry out a non-stop flight to the subtropic winter-quarters. At any rate, the very few recoveries along the first parts of the migration route show that the

Redshank will not usually make long stops on the passage, this holding good of both autumn and spring. There are no recoveries of Danish Redshanks at all in Germany; there is only one recovery in Holland and England, respectively, both from the winter-time. In Belgium there is one early autumn-recovery (24. July) and one very late spring-recovery (28. April); in northern France there are two autumn-recoveries (12. Aug., 20. Aug.), two winter-recoveries (Nov., Dec.) and two spring-recoveries (both from May). These recoveries have all been made along the coastal route. There are only two recoveries along the continental route, both in interior France, *viz* Thiers (Aug.) and dept. Cantal (March). This makes a total of 4 records during autumn-passage, 3 during winter and 4 during spring-passage. This is certainly a very small number compared with the large number of recoveries during autumn-passage in the winter-quarters proper (20 in S. France, 12 in Veneto, etc.). VERHEYEN & LE GRELLE (1950, p. 205) in a recent paper on the migration of the Redshank have drawn attention to the fact that the populations "des Etats baltes et du sud du Danemark manifestent nettement la tendance à traverser transversalement l'Europe pour aboutir le plus rapidement possible à la Méditerranée."

The most important migration route is the continental one, which has rendered 96 recoveries, compared with 58 from the coastal route. The Redshanks, having rapidly crossed the European continent, arrive in July–Sept. in southern France and northern Italy, where they winter preferably in the estuaries of the deltas of river Rhône and Po. However, a considerable number of birds continue the migration further south, possibly owing to a certain crowding in the wintering-places. These birds move partly SE. to southern Italy and to Sicily, partly due S. to Sardinia and—more rarely—to Tunisia, and partly SW. from S. France along the eastern coast of Spain at most as far south as 38° n. lat. The Balcan Peninsula is apparently never touched by the migration. All 19 recoveries from this "southern" area (E. Spain, S. Italy, Sicily, Sardinia, Tunisia) are from the winter-period, only with two exceptions, an autumn-record (Sept.) from S. Italy and a spring-record (April) from Sicily. This evidences that the Redshanks usually

occupy these areas rather late in the autumn and leave them early in spring.

As to the coastal migration route the main winter-quarters are situated in Portugal and SW. Spain, from where there are 12 winter-records, compared with 1–2 in Holland, England and N. France, respectively, 7 in W. France and 2 in N. Morocco. Wintering in Holland, England and N. France is no doubt exceptional, which is evidenced by the very few recoveries in winter in these areas. As shown above (p. 97) the population wintering in W. France displays a steady southward movement during the winter. The winter-quarter in the Iberian Peninsula extends along the entire Portuguese coast and the Spanish coast eastwards to Malaga. There is a considerable gap between this locality and the southernmost place (Torrevieja) reached by the E. Spanish branch of the continental migration route, described above (p. 100). This is due to lack of suitable biotopes in this area. Birds using the coastal migration route sometimes continue from SW. Spain across the Strait of Gibraltar and winter in northern Morocco. This crossing is not common and takes place rather late in the autumn, according to the date of the two Moroccan recoveries (Nov., Dec.).

Apart from the two recoveries of summering birds (one in Salamanca Prov., Spain, and one in dept. Hérault, S. France) there are 152 recoveries abroad of Danish Redshanks, which can be segregated as follows (in %): Recovered as autumn-migrants in Europe 41 %, wintering in Europe 43 %, spring-migrants in Europe 14 % and wintering in N. Africa (Tunisia-Morocco) 2 %.

The Swedish Populations.

The recoveries of Redshanks ringed in Sweden have been recorded in annual lists published by Göteborgs Naturhistoriska Museum (JÄGERSKIÖLD 1929, & 1930–1952) and by Sveriges Ornitologiska Förening (SWÄRDSON 1947–1953). Ringing has been carried out also by Naturhistoriska Riksmuseet, Stockholm; the recoveries have been listed by E. LÖNNBERG in a number of notes in the periodical "Fauna och Flora" and in a comprehensive paper (LÖNNBERG 1935, p. 140–141). In recent years no lists have been published by Riksmuseet. Finally,

TABLE II. Recoveries of Ringed Scanian Redshanks (*Tringa totanus*); arranged according to Locality and Month of Recovery.
Genfangster af ringmærkede skånske Rødben (Tringa totanus), opstillet efter lokalitet og måned for genfangsten.

Locality	Autumn-passage Efterårstræk			Wintering Overvintrende					Spring-passage Forårstræk			Summering Oversommerende		Total Ialt
	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	
Veneto	2	2	4
W. France	1	..	1
S. France	1	1	2
Portugal	1	1
Total (Ialt)...	1	3	1	..	2	1	..	8

Svenska Jägareförbundet have ringed a number of Redshanks, and a single recovery has been published by NOTINI & HÖGLUND (1949). When dealing with the ringing of Swedish Redshanks it is necessary to distinguish between the population of the southernmost part of the country, the province of Scania (Skåne) and the more northern populations.

The Redshanks of Scania.

There are 7 recoveries of birds ringed as nestlings in Scania. To these have been added a single recovery of a bird ringed as nestling in Blekinge (the province east of Scania). The latter bird was recovered in Aug. at Perpignan, dept. Pyrenées-Orientales, S. France. The greater part of the Scanian birds have been recovered in the province of Veneto, NE. Italy, from where there are 4 records: Padova 9. Aug., Adria Nov., Venezia Nov. and Laguna de Venezia 19. Aug. The remaining 3 recoveries have been made in S. France (dept. Hérault, 24. July), in W. France (Arcachon, dept. Gironde, 16 June; a summering bird) and in Portugal (Algarve, Sept.), respectively. All records have been listed in table II. The migration of the Redshanks of Scania does not differ from that of the Danish birds, judging from the rather few recoveries known. When excepting the single summering bird from Gironde there are 7 recoveries, of which no less than 6 have been made on the continental route of migration, only one (in Portugal) along the coastal route. Two birds have been found wintering in Europe (29 %, compared with 43 % in the Danish popula-

tion). The importance of the continental migration route for the Scanian Redshanks has been stressed by P. HENRICI (1946, p. 1461), who is of the opinion that the birds pass along the river Rhine and from Switzerland either along the river Rhône to S. France or along the river Po to the Adriatic Sea. It appears that the Redshank leaves southern Scania (Falsterbo) flying in a SW. direction so that they pass across the Baltic just south of Denmark.

The Redshanks of Öland and further North.

There is a total of 45 recoveries, which all have been listed in table III and shown on the map fig. 2. A considerable ringing of Redshanks has been carried out in the island of Öland, partly of nestlings (by JÄGERSKIÖLD and his assistants), partly of grown-up immature and adult migrants, caught in traps (by SWÄRDSON and assistants). There is apparently no difference between the migration of the two groups, of which the latter no doubt comprises a number of birds of more northern origin besides the indigenous ones. North of Öland very little ringing has been done, and there is only one recovery of Redshank ringed in Jämtland, Norrbotten (Luleå) and Gotland, respectively. All these recoveries fit in a common pattern and they have therefore been united in this study.

Table III has been constructed just as table I–II. The following remarks can be made on the groups of recoveries shown in the table.

Denmark. One ringed as nestling at Luleå, Norrbotten (N. Sweden) recovered at Nissum Fjord, Jutland, 18. Sept.¹⁾

N. Germany. An adult bird trapped and ringed in Öland found freshly dead at Rendsburg, Holstein 19. July (the subsequent year).

N. France. Recoveries of Öland birds: Dept. Calvados 23. May, dept. Somme 24. July, dept. Ille-et-Villaine Sept., Baie-de-Somme April, dept. Côtes-du-Nord Aug., the 2 first ringed as nestlings, the 3 latter ringed as grown-up birds in traps. A bird ringed as nestling on Gotland was recovered in dept. Calvados 1. Sept.

W. France. Recoveries of Öland birds ringed as nestlings: Dept. Vendée 1, dept. Charente-Inférieure 3, dept. Gironde 7. Ringed in Öland as grown-up birds, caught in traps: Vendée 1, Charente-In-

¹⁾ This date was by a mistake given as 18. nov. in my recent book "Fugletrækket og dets gæder", Copenhagen 1953, p. 161.

TABLE III. Recoveries of Redshanks (*Tringa totanus*), Ringed in Öland and farther north in Sweden, arranged according to Locality and Month of Recovery. *Genfangster af Rødben (Tringa totanus), ringmærkede på Öland og længere mod nord i Sverige, opstillet efter lokalitet og måned for genfangsten.*

Locality	Autumn-passage Efterårstræk			Wintering Overvintrende				Spring-passage Forårstræk			Summe- ring Oversom- rende		Total Ialt	
	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI		VII
Denmark	1	1
N. Germany	1	1
N. France	1	1	2	1	1	6
W. France	1	10	5	1	2	6	25
S. France	1	2	2	5
NW. Spain	1	1
Portugal	2	2
SW. Spain	1	1
Morocco	1	1
Senegal	1	..	1	2
Total (<i>Ialt</i>) . . .	3	15	11	..	1	2	5	8	45

fériere 4, Gironde 8. A bird ringed as nestling in Jämtland was recovered in dept. Charente-Inférieure 8. May.

S. France. Recoveries of Öland birds: Dept. Pyrénées-Orientales 17. April, dept. Var 25. April, dept. Tarn Sept., dept. Hérault 7. Aug., dept. Gard 22. Sept., only the first bird being ringed as nestling, the rest as grown-up birds, caught in traps.

NW. Spain. Ringed in Öland as grown-up, recovered at Bilbao 19. Aug.

Portugal. Ringed as nestlings in Öland, recovered at Aveiro Aug., and Lisbon Aug.¹⁾.

SW. Spain. Ringed as grown-up in Öland, recovered at Jerez de la Frontera 29. March.

Morocco. Ringed as grown-up in Öland, recovered in Spanish Morocco 23. May.

Senegal. Ringed as grown-up birds in Öland, recovered at Dakar in Sept., and 460 km NNE. of Dakar 24. Nov.

The migration of the Swedish Redshanks differs considerably from that of the Danish birds and displays several points of interest. While the Danish (and Scanian) population mainly follows the continental migration route, heading almost due south in the autumn, the Swedish population uses the coastal route. It appears from table III that practically all

¹⁾ The recovery at Lisbon was originally published as having been made in Jan., but the correct date of recovery is 28. Aug., according to P. HENRICI (1946, p. 1462).

recoveries have been made along the Northsea and Atlantic coasts of Central and SW. Europe. The only exceptions are 3 autumn-recoveries and 2 spring-recoveries in S. France. The migration route from Öland and Gotland no doubt leads along the Baltic, passing slightly south of Denmark. The recovery of an Öland bird at Rendsburg in the middle of Holstein is of interest in that respect. This shows the peculiar fact that the migration route of the Swedish birds, leading in the autumn from NE. to SW., crosses the route of the greater part of the Danish birds, which goes in a southern direction. This is to be seen on the map fig. 2. A crossing of the migration routes of neighbouring populations or subspecies is a rare phenomenon. I know only of two other instances, viz: *Lanius cristatus lucionensis* L. and *L. c. superciliosus* Lath. in East Asia, and *Dendroica p. palmarum* (Gmelin) and *D. p. hypochrysea* Ridgway in N. America.

The Redshank ringed at Luleå, Norrbotten, N. Sweden, recovered at Nissum Fjord, NW. Jutland, has not followed the general route of migration of the Öland birds, as to be seen in fig. 2. It either followed the migration route across the lake district of Middle Sweden and reached the Northsea coast in northern Jutland, or it crossed Scandinavia to the Norwegian coast which it then followed southwards to Denmark. The significance of the inland route across Central Sweden for the migration of waders (including Redshanks) has been particularly emphasized by SÖDERBERG (1947, p. 290). The migration of the North Swedish Redshanks along the Norwegian coast has been thoroughly dealt with by HENRICI (1946, p. 1462) in his excellent treatise on this species. In this connection the recovery of a Greenshank (*Tringa nebularia* (Gunn.)) 13. Sept. at Harboøre, W. Jutland (not far from Nissum Fjord), is of interest. This bird was ringed in Jämtland, N. Sweden, near the Norwegian border, and has no doubt followed the Norwegian coast southwards to reach the Northsea in N. Jutland.

The Swedish Redshanks differ, further, from the Danish-Scanian ones by the fact that they do not winter in Europe. In the end of Sept. they have all left Europe, while the Danish population has an even greater percentage of recoveries in Europe in winter (43 %) than during the autumn-months

(41 %). As a matter of fact, the recovery of a Swedish bird at Bordeaux, dept. Gironde, W. France on the 1st of Oct. has been put among the Sept. birds in table III, as it obviously was a normal passage-migrant, not a wintering bird. The Swedish Redshanks evidently continue the migration across the Strait of Gibraltar to winter in subtropic and tropical Africa. This is born out by the fact that two recoveries have been made near Dakar in Senegal, while in the Danish material of recoveries, which is $3\frac{1}{2}$ times as large as the Swedish one, there is not a single recovery in the tropics. There is a widespread tendency among northern bird-populations to cross the winter-quarters of the more southern populations and winter still further south than these, but it is rarely seen so distinctly as in the Redshank.

The dates for the autumn-passage of the Swedish birds appear to be very similar to those of the Danish ones. There is a number of very early recoveries, *viz*: Rendsburg, N. Germany, 19. July; dept. Somme, N. France, 24. July; dept. Gironde, W. France, 31. July, and many early August recoveries (2nd, 4th, 5th, 6th, 10th, 10th Aug., all from France). The percentage of recoveries in the three months of autumn-passage is practically the same as in the Danish birds, as shown in the following table:

	July	Aug.	Sept.	Number of Recoveries
Danish	6 %	60 %	34 %	62
Swedish	11 %	50 %	39 %	28

There is, however, a distinct difference in the time of the spring migration between the Danish and Swedish population, which appears from the table below:

	March	April	May	Number of Recoveries
Danish	48 %	38 %	14 %	21
Swedish	13 %	33 %	54 %	15

The main spring migration of the Danish birds takes place in March and is almost finished before May, while the Swedish birds, to the contrary, have hardly arrived in Europe in March and reach a peak in number in May. The dates for the May recoveries of the Swedish birds are: 1st, 5th, 8th, 8th, 14th, 19th,

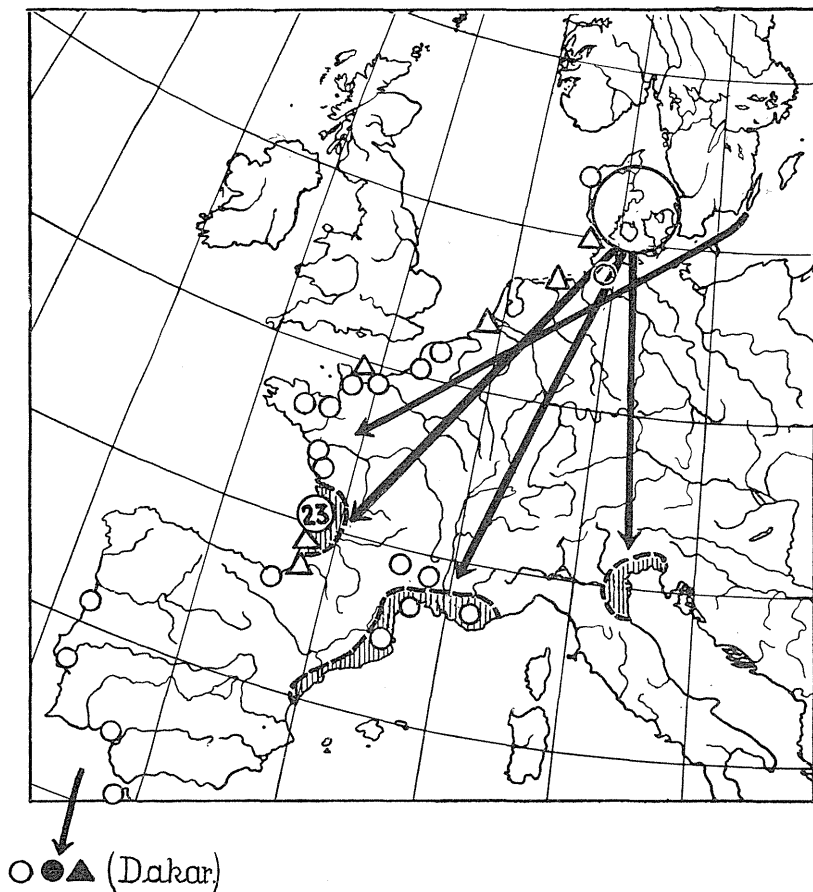


Fig. 2. Recoveries of Redshanks (*Tringa totanus*) ringed in Sweden (circles) and Norway (triangles). Open signatures designate recoveries in migration time, solid signatures recoveries in winter; figures give number of recoveries. The main winter-quarters of the Danish Redshanks are hatched, and the arrows show the crossing of the migration routes used by the Danish and Swedish birds, respectively.

Genfangster af Rødben (Tringa totanus) ringmærket i Sverige (cirkler) og Norge (trekanter). Åbne signaturer viser ringfund i træktiderne, udfyldte signaturer ringfund om vinteren; tallene angiver antal ringfund. De danske Rødbens hovedkvarterer er skraverede, og pilene viser overkrydsningen af de svenske og danske Rødbens trækruter.

23th, 23th of May; the dates of the Danish ones are 3rd and 7th of May (a third specimen is dated as "May" only). The late spring migration corresponds with the fact that the arrival at the Swedish breeding-places takes place as late as

from mid-April to early May in Middle Sweden (Småland, Uppland) and mid-May in N. Sweden (HENRICI 1946, p. 1462).

Apparently the Swedish birds travel northwards at a somewhat slower rate than the Danish ones, judging from the fact that the number of spring recoveries of Swedish birds (15) constitutes more than half the number of the autumn recoveries (28), while among the recoveries of the Danish birds the number in spring (21) is only one third of that in the autumn (62).

The Norwegian Population.

The recoveries of Redshanks ringed in Norway have been published in annual lists by H. TH. L. SCHAANNING (1931-49) and H. HOLGERSEN (1950-52). The ringing of the Norwegian Redshanks has been carried out in Jæren in southernmost Norway; all birds were trapped in the autumn as grown-up birds, for the greater part probably being on migration. Only 8 recoveries abroad are known, and according to them the migration route leads along the W. coast of Jutland and continues along the Northsea and Atlantic coast of Europe, south to tropical Africa, just as was the case in the Swedish Redshanks. The recoveries are situated on the entire coastal migration route with almost regular intervals from Denmark right down to Senegal, *viz*: Ballum, SW. Jutland, Denmark, 20. Sept.; Frisian Islands, NW. Germany, Sept.; Zealand, Holland, 15. Sept.; dept. Calvados, N. France, Sept.; dept. Charente Inférieure, W. France, 10. May¹); dept. Gironde, W. France, 9. Oct.; dept. Landes, W. France, May; Dakar, Senegal, 21. Oct. The recoveries have been plotted on the map fig. 2 and have been enumerated in table IV.

The autumn migration takes place later than in the Danish and Swedish populations, judging from the autumn recoveries, which were all made in Sept., while the Danish-Swedish birds started the migration in July and reached the greatest density as early as in Aug. According to LÖVENSKIOLD (1947, p. 732) the autumn-passage through Norway "takes place in the latter half of Aug. and the first half of Sept.; a few specimens stay till Oct." This agrees with the late dates of the recoveries. It is noteworthy that the Redshanks of the alpine tracts of

TABLE IV. Recoveries of Redshanks (*Tringa totanus*), Ringed in Norway, arranged according to Locality and Month of Recovery.

Genfangster af Rødben (Tringa totanus) ringmærkede i Norge, opstillet efter lokalitet og måned for genfangsten.

Locality	Autumn-passage Efterårstræk			Wintering Overvintrende					Spring-passage Forårstræk			Summe- ring Oversom- rende		Total Ialt
	VII	VIII	IX	X	XI	XII	I	II	III	IV	V	VI	VII	
Denmark	1	1
NW. Germany	1	1
Holland	1	1
N. France	1	1
W. France	1	2	3
Senegal.....	1	1
Total (<i>Ialt</i>)...	4	2	2	8

N. Sweden, which no doubt migrate along the Norwegian coast (cf. p. 105, above), are known to stay in the breeding area until mid-Aug., this holding good of both adult and immature birds (HENRICI 1946, p. 1462). The specimen recovered in Gironde 9. Oct. must be regarded as a normal passage-migrant and not as a winter-visitor, on account of the late migration of the Norwegian birds. The only recovery of a wintering bird is that from Dakar. It is very interesting that among only 8 recoveries of Norwegian birds one is from tropical Africa, while among the 154 recoveries abroad of the Danish birds not a single came from the tropics. This shows that the Norwegian birds, as well as the Swedish ones, mainly winter in the tropical parts of Africa, while the Danish population remain in the Mediterranean area.

According to the only two recoveries in spring, both in May, the spring migration takes place as late as in the Swedish birds, mentioned above (p. 106).

Other European Populations.

Ringing of Redshanks has been carried out in a number of European countries, but the number of recoveries is much inferior to that of the Scandinavian birds. Nevertheless, the

¹) This recovery has not yet been published, and the information was kindly given me by dr. H. HOLGERSEN (*in litt.*), too late, however, to plot it on the map fig. 2, as the drawing of this map was finished some time earlier.

ringing records give some hints as to the segregation in winter of the different Redshank populations of Europe.

E. Germany. The migration of the E. German Redshanks appears to be very similar to that of the Danish birds. In the *Atlas* published by SCHÜZ & WEIGOLD (1931, Tafel 68) there is a recovery of a Pomeranian bird from Bouches-de-Rhône, S. France (Aug.) and Veneto, N. Italy (Feb.), respectively; further a recovery of a bird from Silesia in Veneto (Oct.). NIETHAMMER (1942, 3, p. 196) adds a recovery of a bird from Brandenburg at Genova, N. Italy (March). Here can be added a recovery of a bird from Checkoslovakia in Veneto. According to Prof. R. DROST (*in litt.*) a bird from Anhalt on the river Elbe was recovered at Modena, N. Italy (March).

W. Germany. Prof. R. DROST has kindly given me (*in litt.*) informations about recent recoveries of birds from NW. Germany. Of 4 birds from the German Northsea coast (3 Wangeroog-West, 1 Elms-horn, Holstein) two were recovered in dept. Gironde, W. France, both in March, one (a wounded bird) in Oost Flandern, Belgium in Oct., and one in dept. Bouches-de-Rhône, S. France in March, *i. e.* the greater part has chosen the coastal migration route, as was to be expected. Nothing definite can be said about the winter-quarters of the NW. German birds, but when comparing with the Dutch and Belgian birds it is reasonable to assume that they winter in the western part of the Iberian Peninsula.

Holland. Dr. G. C. A. JUNGE has kindly given me the following information (*in litt.*) about the movements of the Dutch population: "Winter-recoveries of the Dutch breeding-birds of the Redshank are not numerous. Five out of nine indeed come from Portugal and another from southern Spain. This can prove that this is the main winter-quarter. Two others (Jan. and Dec.) come from NW. France, which may be connected with mild winters. A quite recent record is a Feb. bird from Dalmatia and two April birds recovered in dept. Aude, S. France and in W. Africa, respectively. This may show that a part of our population winters further south. But as long as we have no more recoveries it is difficult to say if these are exceptions." It appears that the main bulk of the population uses the coastal route and winters in Portugal and S. Spain.

Belgium. There are a few recoveries of Belgian birds along the French coasts (dept. Pas-de-Calais, N. France, 11. June (summering); dept. Loire-Inférieure, W. France, 5. May & 22. Jan. (VERHEYEN 1948, p. 192), dept. Gironde, W. France, 17. Aug. (LIPPENS 1952, p. 326)) and one from Cádiz, SW. Spain, 12. Dec. (SAEZ-ROYUELA 1952, p. 44). One recovery was made in England (Essex, Aug.). Finally, a summering bird was recovered 6. June near Stuttgart in S. Germany. According to this material the migration of the Belgian birds does not differ from that of the Dutch ones, described above.

Hungary. There are 7 winter-records (Oct.-Feb.) given in the

Atlas by SCHÜZ & WEIGOLD (*l. c.*) distributed over southern Yugoslavia (2), southern Italy (2) and Tunis (3), all showing a distinct SW. direction. Besides, there is a recovery from Crete (Nov.), which shows a SE. direction and somewhat falls outside the main migration route. In a recent paper by VERHEYEN & LE GRELLE (1950, p. 204) on the migration of the Redshank no recent recoveries have been added.

England. The British Redshank (*Tringa totanus britannica* Mathews) is partly resident. A number moves more or less to the south to winter along the S. coast of England or cross the Channel to N. France, seldom reaching W. France. The Scotch birds move generally to Ireland. These conclusions are based on a rather extensive ringing material; cf. also WITHERBY *et al.* 1940, 4, p. 327. Recoveries have shown that birds from northern counties may reach S. England as early as the end of July and N. France in Aug.

Iceland. The Iceland Redshank (*Tringa totanus robusta* (Schiøler)) winters mainly in the British Isles, most commonly in Scotland, where the greater part of the recoveries has been made. A fair number winters in the northern parts of Ireland and in western England. A minority stay in Iceland, where they winter in the southern parts of the country. In addition, the Iceland Redshank appears to be not uncommon along most of the Northsea coasts. In Belgium it appears to be a regular winter-visitor (VERHEYEN 1948, p. 196). There is a number of records from Holland and NW. Germany (Heligoland), in which latter country it is "probably not rare" (NIETHAMMER 1942, 3, p. 199). On the other hand, it is not mentioned at all in the new list of birds of France (MAYAUD 1953, p. 23). In Denmark it is a regular, but rather local winter-visitor (SALOMONSEN 1953, p. 126, and unpublished material), and the same appears to be the case in S. Norway (LØVENSKIOLD 1947, p. 733). A small part of the Iceland population moves further south along the Atlantic coasts of W. Europe, and there is a single recovery in Morocco. This is, however, an exception.

In fig. 3 are shown the main winter-quarters of a number of European Redshank populations, based on the ringing results set forth above. Ringing has not been carried out in any other countries than those mentioned above. There is an old recovery in England of an alleged Russian bird, but this record has rightly been discarded by SCHÜZ & LÖHRL (1954, p. 2). I want to emphasize that the map fig. 3 shows the *main* winter-quarters only. Outside the areas drawn on the map there is a fair number of more peripheral recoveries in winter-time. I wish especially to draw the attention to W. France, where birds from Holland, Belgium, NW. Germany, Denmark and England winter, but this area is not the main winter-quarter of any of these populations. Purely exceptional winter

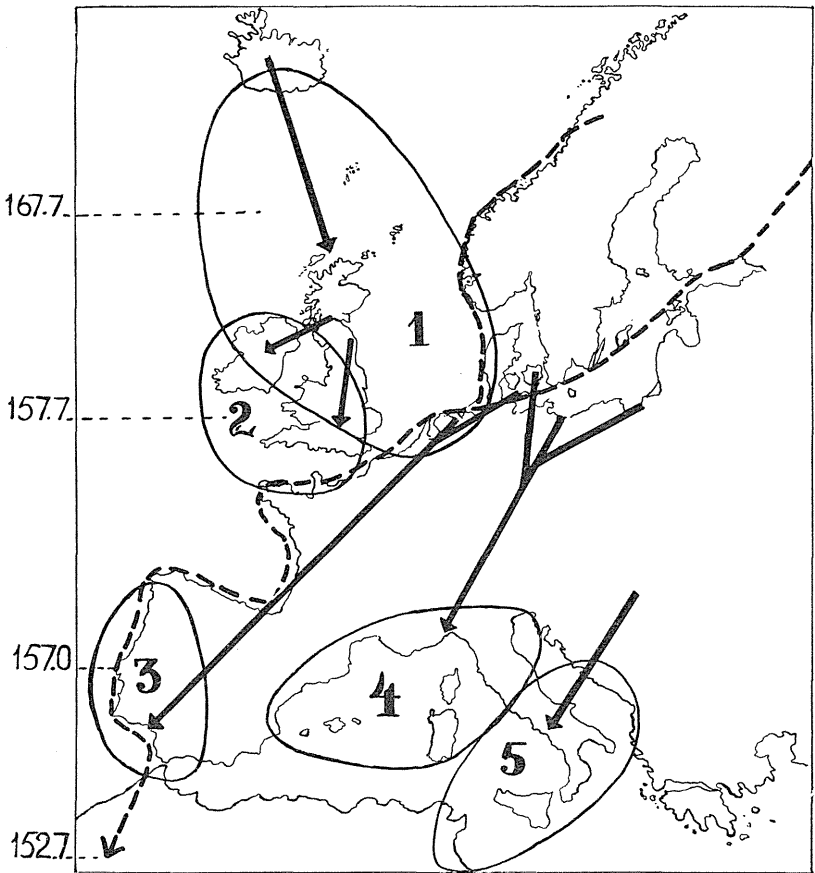


Fig. 3. Main winter-quarter of various European populations of Redshank (*Tringa totanus*). 1. Iceland, 2. British, 3. Belgian-Dutch-W. German, 4. Danish-E. German, 5. Hungarian population. Broken line: Migration route of Swedish and Norwegian (? and Russian) populations to tropical Africa. Figures inserted at left give average wing-length of the Redshanks wintering in the area in question.

Hovedvinterkvarter for forskellige europæiske populationer af Rødben (Tringa totanus). 1. Islandske, 2. Britiske, 3. Belgisk-Hollandsk-Vesttyske, 4. Danske-Østtyske, 5. Ungarske populationer. Den stiplede linie angiver de svenske og norske (? og russiske) populationers trækvej til Afrika. Tallene tv. er middelvingelængden for de pågældende områder overvintrende Rødben.

recoveries, like the Danish ones in Holland and England, or the Iceland one in Morocco, could of course not be considered in the map. There is, naturally, some overlap everywhere in the wintering areas of the different populations. However, these populations are not natural units, but have been chosen

for practical reasons. Presumably there is a gradual replacement of birds from new populations when moving from one part of the winter-range to another, *i. e.* from southern Italy to southern France populations originating from Hungary, Checkoslovakia, E. Germany and Denmark will replace each other.

It is interesting that no E. European Redshanks winter in the British Isles. There are only two recoveries of continental birds in England; apart from the Danish bird, mentioned above (p. 98), a Belgian one recovered at Essex 7. Aug. (VERHEYEN & LE GRELLE 1950, p. 205). These authors remark that "Les Gambettes du continent semblent éviter de passer par la Grande-Bretagne". The recoverer of the Danish specimen, LtCol. D. K. WOLFE-MURRAY informs me (*in litt.*) that "I remember on picking the bird up that it struck me as being in poor condition, and was decidedly thinner than others in the same area". This may indicate that this specimen had erred about, off its normal migration route, in a state of exhaustion.

The map fig. 3 shows the distribution in winter in Europe only and does not consider the African part of the winter-range. The Redshanks wintering in tropical Africa originate from Scandinavia and no doubt also from Russia. The migration route chosen by the Scandinavian birds is shown on the map as a broken line, which is continued northwards at the most probable route of the N. Russian birds. The migration route along the Norwegian coast, which ends on the map in the Central Scandinavian mountains, could have been extended northwards right up to North Cape or further, as Redshanks are known to breed right to northernmost Norway. Apart from the Scandinavian recoveries in tropical Africa (Senegal) there is only one other recovery there, *viz* a Dutch bird from Dakar (8. April). This recovery is, however, situated so far south of the usual winter-quarter of the Dutch population that it must be regarded as a mere exception.

Discussion and Conclusion.

The European Redshanks offers a beautiful example of a species in which the different populations in their winter-ranges attempt to spread over so wide an area as possible, in order to avoid more crowding (population pressure) and resultant competition for food than necessary. This dispersal has been achieved by a spatial division of the available winter-quarters among the populations and has been favoured by selection during winter-time. Selection has produced hereditary differences in direction and choice of migration route, in time and speed of migration, *i. e.* in the strength of the urge or instinct of migration, and finally in the adaptation to local climatic and other ecological factors.

In order to obtain the optimum balance between the wintering populations complicated rearrangements of the populations have been necessary. In western Europe the populations are displaced in the autumn in a parallel way, the northernmost population (the Iceland birds) wintering at the Atlantic and Northsea coasts north of the British population, and this latter wintering north of the W. German-Dutch-Belgian population. In eastern Europe the migration pattern differs widely. East of the river Elbe, which acts as a "migratory divide" (German: *Zugscheide*) the Redshanks use a continental migration route, which leads in a southerly direction through the mainland. The Danish population is on the verge; a number uses the western coastal route, in common with the W. German-Dutch-Belgian birds, but the majority follows the continental route. However, the Scandinavian (Swedish-Norwegian) birds do not winter north of the Danish-German ones, as should be expected in analogy with the W. European birds, but to the contrary, south of them, in tropical Africa. In this way the populations so to speak play at leap-frog, a phenomenon found also in a number of other species, but rarely so distinctly developed as in the Redshank.

The leap-frog migration of the Scandinavian birds might have been accomplished by a straight southward flight, heading directly for Africa. The Scandinavian populations, however, have chosen to follow the coastal route, leading along the southern Northsea coast and the Atlantic coast of France and

the Iberian Peninsula. This has resulted in the peculiar crossing of the migration routes south of Denmark, the Danish birds moving southwards, the Baltic ones westwards through northern Germany. The Danish population, the migration of which is the best known, has a remarkable position, situated in between the two flows of Scandinavian birds, both heading for Africa, the Norwegian one along the western border of the country, the Baltic one just south of the country. The interesting fact is that the Danish population follows neither of the streams, but crosses the Baltic one almost at a right angle, as can be seen in fig. 3.

The Scanian birds have a similar migration pattern as the Danish-German ones, and the migratory divide which separates the Danish-Scanian birds from the Swedish-Norwegian ones, runs immediately east and north of Scania forming an extraordinarily sharp and clear-cut break.

The separation of the different populations in the winter-quarters is not absolute. In most places there is some mixing of the populations, least in tropical Africa, where the winter-visitors consist almost exclusively of Scandinavian birds, and in the Northsea area (Scotland, NW. Germany, Denmark, S. Norway), where the winter-visitors are practically all of Iceland origin. The greatest mixing no doubt takes place in W. France, where birds from Denmark, W. Germany, Holland, Belgium and England gather in winter-time.

Modern genetics has shown that geographical isolation is a *conditio sine qua non* for speciation (cf. MAYR 1942, p. 147). In my opinion a spatial segregation of various populations in winter is highly significant from an evolutionary point-of-view, a fact which has generally been overlooked. I intend to treat this topic in a future paper and therefore shall not go into details here. I want, however, to stress a few points. In analogy with the well-known terms allopatric and sympatric species I here propose the terms allohiemic and synhiemic. Populations (or subspecies) are *allohiemic* when they are separated in their winter-quarters, *synhiemic* when they are united on the wintering grounds. Synhiemic are most ducks, terns and sea-birds, allohiemic the greater part of the terrestrial birds. The distinction is one of degree; allohiemy is seldom complete and does

not need to be so in order to affect evolution. In winter (which here means the non-breeding season) selection is the only genetic factor involved, and its activity cannot be hampered or impeded by disturbing mutations or gene-flow.

It appears from the map fig. 3 that the populations of the Redshank show a marked allohiemy, the winter-quarters of the greater part of the populations being very well separated. The existence of the "leap-frog" migration, of the migratory divide in Central Europe, and of the overcrossing migration-routes south of Denmark do not derange the pattern. Selection has formed a firm and almost rigid system.

Selection in the winter-quarters has given rise also to morphological differences among the populations, owing to the high degree of allohiemy in these birds. HARRISON (1944, p. 493) has studied the European races of the Redshank. On the basis of his figures the variation in wing-measurements can be shown as follows:

Norwegian, Estonian:	10 ♂♂	148–158	(average 152.7 mm)
Danish:	6 ♂♂	152–162	(– 157.0 –)
English:	10 ♂♂	152–166	(– 157.2 –)
Scotch:	10 ♂♂	151–165	(– 157.7 –)
Iceland:	7 ♂♂	165–172	(– 167.7 –)

The average figures have been placed in fig. 3 off the wintering area of the proper populations. It is distinctly to be seen that the wing-length increases to the north and thus offers an example of the so-called BERGMANN'S rule (cf. RENSCH 1929, p. 133). This variation is due to selection in the winter-quarters¹). When the populations are compared in the breeding-areas the variation in size makes no sense; *e. g.* in the north, about the Arctic Circle, are found both the biggest birds (Iceland) and the smallest ones (Norway). When the populations are arranged in the winter-quarters this discrepancy is removed. I may add that selection in the breeding-area is of course also important, particularly if the breeding-population is isolated as is the case in the Iceland birds. The combined effect of selection in breeding and winter area accounts for the comparatively great morphological difference between the Iceland Redshanks and

¹) Some other instances of morphological differences due to selection in the winter-quarters are given by SALOMONSEN (1951, p. 184).

the other populations, a difference which is great enough to separate the Iceland birds as a well-defined subspecies.

The population of Great Britain, isolated also, forms another subspecies, characterized by its incomplete breeding-dress, but in winter-plumage identical with the other populations. The variation in the nuptial plumage forms a cline from England to Scandinavia, as shown by HARRISON (1944, p. 499). This cline is due to factors working in the breeding areas only, and selection in the winter-quarters is not involved.

Addendum.

After this paper has been finished, some new recoveries of Redshanks ringed in Denmark have been made, *viz*: dept. Bouches-du-Rhône, S. France, 1. Feb. and 7. Feb. (both shot); dept. Calvados, N. France, 28. Jan. (shot); Suffolk, England, 4. Feb. (found dead). A further interesting recovery was a bird recorded on the island of Samsø, Denmark 5. March, showing a very early return to the breeding area. All five birds were ringed as grown-up birds on Amager, caught in traps.

Summary.

Recent ringing in Scandinavia has revealed some new and interesting facts of the movements of the Redshank (*Tringa totanus* (L.)). The conclusions drawn in this paper are mainly based on the considerable number of recoveries.

All recoveries of Redshanks ringed in Denmark have been listed on the map fig. 1 and have been arranged in table I in a number of groups in accordance with the situation of the migration routes and the winter-quarters. Each group of recoveries has been briefly dealt with on p. 96-98.

The recoveries show that there is more than one migration route. One part of the Danish population moves along the European sea-coasts, passing Holland and France and continuing to Spain and Portugal. Another part moves across the inland, heading directly for the Mediterranean coast of France and the Adriatic coast of Italy. The distinction between a coastal (Atlantic) route and an interior (continental) route is found in other Danish birds also, *e. g.* *Philomachus pugnax* and *Tringa glareola*. The most important migration route of the Danish Redshanks is the continental one, which has yielded 96 recoveries, compared with 58 from the coastal one.

The autumn-migration of the Danish Redshanks takes place very rapidly, no doubt often in one stretch from Denmark to the winter-

quarter. The arrival there takes place usually in Aug., but there are some extremely early recoveries, which show that the winter-quarter is sometimes reached in July already (earliest recovery: 28. July).

The main wintering grounds of the birds using the continental route are southern France and northern Italy, but a considerable number continues to southern Italy, Sardinia, Sicily and Tunisia, and along the eastern coast of Spain. The main winter-quarter of the birds moving along the coastal route is the Atlantic coast of the Iberian Peninsula, but a fair number remain in W. France. The wintering grounds in the more southern areas (Portugal, Spain, S. Italy, Tunisia, etc.) are occupied later in the autumn than the more "northern" ones (W. and S. France, N. Italy); cf. p. 96-98 and the table p. 98.

There are 8 recoveries of birds ringed as nestlings in Scania, S. Sweden; they are listed in table II. According to this meagre material the migration of the Scanian birds does not differ from that of the Danish ones. By far the greater part of the recoveries (85 %) has been made on the continental route of migration. Winter-recoveries are known from N. Italy.

All recoveries of Redshanks ringed in the island of Öland and farther north in Sweden have been listed in table III and plotted on the map fig. 2. Particulars on the individual recoveries are given p. 103-104. According to the ringing results (45 recoveries abroad) the Redshanks ringed in Öland and farther north in Sweden differ in their migration from the Danish-Scanian birds in the following points: The coastal route is used by almost all birds (only a few recoveries in S. France); the migration route leads from the Baltic south of Denmark to the German Northsea coast and in this way crosses the migration route, leading south, of the Danish-Scanian birds, as shown in fig. 2. The Redshanks of northernmost Sweden follow on their migration the Norwegian coast and join in the Wadden Sea the birds using the Baltic route. The Swedish birds do not winter in Europe, but continue to tropical Africa. The time for the autumn-passage of the Swedish birds is the same as that of the Danish birds (cf. table on p. 106), but the spring migration takes place considerably later (cf. table on p. 106).

Recoveries of Norwegian Redshanks (a total of 8) are shown also in fig. 2, and are, besides, listed in table IV. According to these recoveries the Norwegian birds follow exclusively the coastal migration route and winter in tropical Africa, as did the Swedish birds. The southward migration in the autumn takes place distinctly later in the Norwegian than in the Danish and Swedish birds.

Ringing of Redshanks has been carried out in a number of other European countries. The recoveries of birds ringed in E. Germany, NW. Germany, Holland, Belgium, Hungary, England and Iceland are described on p. 110-111. The main winter-quarters of the different European Redshank populations, so far as known, are shown on the map fig. 3, where also the coastal migration route of the Swedish and Norwegian birds is given. The map shows that the Redshank popula-

tions in their winter-range attempt to spread over so wide an area as possible in order to avoid competition for food. This development has been favoured by selection in the winter-quarters. The distribution in winter forms a complicated pattern: In W. Europe the populations winter at the Atlantic coasts in the same order in which the breeding areas are situated (Iceland birds north of British birds, etc.); cf. fig. 3. East of the river Elbe the Redshanks use the continental route leading southwards to the Mediterranean coasts of France and Italy. The Danish population is on the verge. The Swedish and Norwegian populations winter in Africa, south of all the other populations, in this way making a "leap-frog" migration. Their migration becomes still more complicated by the fact that they do not fly straight south over the continent but use the coastal route, in this way crossing the southward migration route of the Danish-Scanian birds.

The spatial segregation of the different populations in the winter-quarters no doubt is of evolutionary importance. Selection will tend to adapt the different populations to the local climatic and ecological conditions. The terms *allohiemic* and *synhiemic* are introduced. Populations (or subspecies) are *allohiemic* when they are separated in their winter-quarters, *synhiemic* when they have a common winter-quarter. The populations of the Redshanks show a marked *allohiemy*. Only in species with *allohiemic* populations selection in the winter-quarters is capable of producing geographical units differing in physiology and even in morphology. In the Redshank the geographical variation in wing-length is due to selection in the winter-grounds. When arranged in the winter-quarters the populations follow the rule of BERGMANN, *i. e.* the wing-length increases to the north (with increasing cold), but when arranged in the breeding areas the populations do not in their size variation follow any ecological rule. Average wing-lengths, based on measurements taken by HARRISON, are inserted on the map fig. 3, where the populations are arranged in their winter-quarters.

In an addendum 5 new recoveries of Redshanks ringed in Denmark are mentioned; they fit in with the migration pattern of the Danish population, described above.

DANSK RESUMÉ

De europæiske Rødbens (*Tringa totanus* (L.)) trækforhold.

I de senere år er der i de skandinaviske lande foretaget en udstrakt ringmærkning af Rødben (*Tringa totanus*), først og fremmest i Danmark, hvor især Hr. MARDAL JENSEN og gross. P. THOLSTRUP ved fangst i fælder på Amager har udført et overordentligt stort og udbytte- rigt arbejde. Ringmærkningen har afsløret en række interessante forhold i Rødbenets træk, og denne afhandling beskæftiger sig først og fremmest med genfangsterne af de skandinaviske Rødben og de slutninger, som de giver anledning til at drage.

Alle genfangster af Rødben ringmærket i Danmark er afsat på kortet fig. 1, og er i tabel I opstillet i et antal grupper efter forløbet af trækket og beliggenheden af vinterkvarteret. Genfangsterne viser, at der er mere end ene trækroute. En del af de danske Rødben trækker langs V. Europas havkyster, idet de passerer Holland og Frankrig og fortsætter til Spanien og Portugal. En anden del trækker tværs over fastlandet, direkte mod den franske Middelhavskyst og den italienske Adriaterhavskyst. En adskillelse mellem en atlantisk kystrute og en indre fastlandsrute findes også hos andre danske fugle, f. eks. Brushane (*Philomachus pugnax*) og Tinksmed (*Tringa glareola*). Fastlandsruten er langt den vigtigste for de danske Rødben, idet 96 genfangster falder på den mod 58 på kystruten.

De danske Rødbens efterårstræk går meget hurtigt for sig, sikkert ikke sjældent i eet stræk fra Danmark til vinterkvarteret. Ankomsten dertil finder i reglen sted i aug., men der findes nogle meget tidlige genfangster, som viser, at vinterkvarteret undertiden nås allerede i juli (tidligste genfangst: 28. juli).

Hovedkvartererne for de fugle, som anvender fastlandsruten er Sydfrankrig og Norditalien, men et betydeligt tal fortsætter til Syditalien, Sardinien, Sicilien og Tunis samt langs Spaniens østkyst. Hovedvinterkvarteret for de fugle, som trækker ad kystruten er Pyrenæerhalvøens atlantiske kyster, men et vist antal forbliver i Vestfrankrig. Vinterkvartererne i de mere sydlige områder (Portugal, Spanien, S. Italien, Tunis, o. s. v.) opsøges senere om efteråret end de mere »nordlige« (V. og S. Frankrig, N. Italien); se også tabellen p. 98.

Der findes 8 genfangster af Rødben ringmærket som unger i Skåne; de er opstillet i tabel II. Ifølge dette ret lille materiale afviger de skånske fugles træk ikke fra de danskes. Størstedelen af genfangsterne (85%) er gjort på fastlandsruten. Vintergenfangster foreligger fra N. Italien.

Alle genfangster af Rødben ringmærket på Öland og længere mod nord i Sverige er opstillet i tabel III og er vist på kortet fig. 2. Ifølge ringmærkningsresultaterne (45 genfangster i udlandet) afviger disse svenske Rødben på flere måder i deres træk fra de dansk-skånske. Kystruten anvendes af praktisk talt alle fuglene, idet der kun foreligger ganske enkelte genfangster fra Sydfrankrig, mens alle andre er fra kystruten. Denne fører fra Østersøen syd om Danmark til den tyske Nordsøkyst og krydser på denne måde den sydgående fastlandsrute, som benyttes af de dansk-skånske Rødben, således som det er vist fig. 2. Rødbenene fra det nordligste Sverige følger på deres træk den norske kyst og forener sig i Vadehavet med de fugle, som følger Østersøruten. De svenske Rødben overvintre ikke i Europa, men fortsætter til tropisk Afrika. Tidspunkterne for de svenske Rødbens efterårstræk afviger ikke fra de danske fugles (se tabellen på p. 106), mens forårstrækket foregår betydeligt senere (se tabellen på p. 106).

På fig. 2 er også vist genfangsterne af norske Rødben (ialt 8), der desuden er opstillet på sædvanlig måde i tabel IV. Ifølge disse genfangster følger de norske fugle udelukkende kystruten og overvintre

i tropisk Afrika, ligesom de svenske fugle. Efterårstrækket finder sted betydelig senere hos de norske end hos de danske og svenske Rødben.

Ringmærkning af Rødben har været udført i en række europæiske lande. Genfangster af fugle mærkede i Østtyskland, Nordvesttyskland, Holland, Belgien, Ungarn, England og Island er gennemgået p. 110–111, og hovedvinterkvartererne for disse forskellige Rødbenpopulationer er, så vidt de kendes, afsat på kortet fig. 3, hvor også de svenske og norske Rødbens trækrute langs kysterne (den stiplede linie) er angivet. Kortet viser, at Rødbenspopulationerne i deres vinterkvarter har forsøgt at fordele sig over så store strækninger som muligt for at undgå næringskonkurrence. Denne udvikling er blevet begunstiget af selektion (naturlig udvælgelse) i vinterkvartererne. Rødbenets vinterudbredelse danner et kompliceret mønster: I Vesteuropa overvintrer populationerne i den samme rækkefølge i nordlig-sydlig retning, som ynglepladserne er beliggende (d. v. s. de islandske fugle nord for de engelske, o. s. v.); se fig. 3. Øst for Elben anvender Rødbenene fastlandsruten, som fører mod syd til Frankrigs og Italiens Middelhavskyster. Danmark danner et overgangsområde, idet trækdeleren går gennem landet; de fleste danske Rødben benytter fastlandsruten, en del dog kystruten. De svenske- og norske populationer overvintrer i Afrika, syd for alle de andre populationer, idet de ligesom »springer buk« over de andre. Deres træk bliver endnu mere indviklet derigennem, at de ikke flyver stik mod syd over det europæiske fastland, men anvender kystruten og på denne måde krydser de dansk-skånske Rødbens sydgående rute, som det ses på fig. 2 og 3.

Den rumlige fordeling af de forskellige Rødbenspopulationer i vinterkvartererne er utvivlsomt af betydning for evolutionen. Selektionen vil tilstræbe en tilpasning hos de forskellige populationer til de lokale klimatiske og økologiske betingelser. Populationerne indenfor en art kan være *allohiemiske* eller *synhiemiske*. At de er allohiemiske vil sige, at deres vinterkvarterer er geografisk adskilte, mens de kaldes synhiemiske når de har fælles vinterkvarter. Populationerne hos Rødbenet viser en udpræget allohiemi. Det er kun hos arter med allohiemiske populationer, at selektionen i vinterkvartererne er i stand til at frembringe geografiske grupper, som indbyrdes afviger i deres fysiologi eller endog i deres morfologi. Hos Rødbenet skyldes den geografiske variation i vingelængden selektion i vinterkvartererne. Når populationerne befinder sig i vinterkvartererne, følger de BERGMANN'S regel, d. v. s. vingelængden tiltager mod nord (i tiltagende kulde), mens størrelsesvariationen ikke følger nogen økologisk regel, når populationerne befinder sig på ynglepladserne. Vingelængdens middeltal, baseret på målinger gjort af HARRISON, er indsat på kortet fig. 3, hvor populationerne er anbragt i deres vinterkvarter.

I en tilføjelse omtales 5 nye ringfund af danske Rødben; de passer ind i den beskrivelse af de danske Rødbens træk, som er givet nedenfor.

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