DANISH REVIEW OF GAME BIOLOGY Vol. 8 no. 8

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by
IB CLAUSAGER

Med et dansk resumé: Skandinaviske skovsneppers *(Scolopax rusticola)* træk

Резюме на русском языке
Миграция скандинавского вальдшнепа
(*Scolopax rusticola*)

COMMUNICATION NO. 122 FROM VILDTBIOLOGISK STATION
Vildtbiologisk Station, Kalø, 8410 Rønde, Denmark
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Introduction

During the period 1968–1972, the Game Biology Station carried out a study of the occurrence and shooting utilization of the woodcock *(Scolopax rusticola)* in Denmark. The results were presented in a preliminary report (CLAUSAGER 1972a), and parts of the study were later published (CLAUSAGER 1972b, 1973a, 1973b).

The present paper concerns the migration of woodcock breeding in Norway, Sweden, Finland and Denmark, based on ringing results from these countries. Recoveries were also used for analyses of the average annual mortality and turnover rates in the Scandinavian population. Recoveries of adult woodcock ringed during migration and in winter on Heligoland (W Germany), in Holland and in the British Isles were then compared with recoveries of woodcock ringed in Scandinavia.

The normal sequence of migration, and migration through Denmark in each of the years 1969–1972, are described on the basis of bagged woodcock material. This source was also used for analyses of the influence of weather conditions on the actual sequence of migration. From autum 1970 until spring 1972, wing feathers (outermost primaries) were collected for analyses of the age distribution during migration, while the sex ratio among migrating individuals was studied by examining bagged birds.

The author would like to thank H. HOLGERSEN and S. MYRBERGET, Norway, S. ÖSTERLÖF, Sweden, I. STÉN, Finland, N. O. PREUSS and S. ROSENDAHL, Denmark, F. GOETHE, W Germany, B. J. SPEEK, Holland, and R. SPENCER, England, for kindly making recovery material available. In addition thanks are due to those, who made their Game Books available, or contributed other information. Dr. R. RUSSEL is thanked for translating the manuscript into English. Ms. M. SHORTEN has given valuable criticism of the paper.

Previous studies of woodcock migration

Woodcock migration has long been a subject of attention and interest, as the species is still considered by sportsmen throughout Europe to be one of the most noble species of game. Taken together with the economic importance of woodcock, especially in the past, this has led to migration conditions being discussed on several occasions in articles and contributions, which have not always been in agreement. The papers can roughly be divided into three main groups:

1) The occurrence of woodcock during migration and in winter.

As early as the 1880's in Denmark, reasonably organized records were kept by estates to examine the degree and sequence of migration (DANSK JAGTTIDENDE 1885 ..). Similar descriptions from other countries also exist (LA MORDORÉE 1953–1974).

2) Migration movements of woodcock, based on ringing results.

Some of the recoveries obtained in Europe up to 1931 are summarized by SCHÜZ & WEIGOLD (1931). Since then, woodcock migration has been discussed by several authors, such as LÖNNBERG 1931 and 1935 and ALEXANDER 1946. In recent years, KRAFFT (1972), GARAVANI (1972), FADAT (1972) and SHORTEN (1974) have presented data on woodcock migration. Recoveries of individuals ringed in Finland, Sweden and Norway are reported by GARAVANI, while FADAT mainly deals with recoveries in France, and SHORTEN illustrates movements by first-year birds from Scandinavia to Britain and Ireland.

3) Conditions affecting migration itself.

THIENEMANN (1912) described the autumn migration of 1909 and 1910 in East Prussia, and mentioned that woodcock always arrive on an easterly wind. The birds appeared to continue travelling if the nights became cold and clear, while if the weather was mild and misty, they remained for several days.

PITTET (1920, 1923) attempted to discover a relationship between the number of birds migrating and the weather conditions. He proposed a formula in which the average number of birds observed in an area is proportional to a meteorological index which includes temperature conditions in NE Europe. The formula was in accord with results for the years studied. PITTET was of the opinion that temperature is an essential factor in migration.

WEIGOLD (1924) held the view that wind frequently affected the route flown by woodcock and that such drift explained why different numbers of birds passed through a given area from one year to another. WEIGOLD also maintained that two types of migration exist; one, a concentrated, rapid migration, initiated by conditions of clear weather with high barometric pressure, a drop in temperature, and N–NE winds, and the other a more leisurely migration with interruptions, occurring during mild, unsettled weather.

KLINGE (1925), in discussing winter migration, was of the opinion that snow-fall had a much greater effect on the migratory impulse than did a drop in temperature.

SCHENK (1924) studied spring migration in relation to weather conditions; he discovered that low pressure over NW Europe was associated with considerable migration of woodcock in Hungary. This is explained by the SW and S winds caused by low pressure in this area bringing warm air from the Atlantic into Hungary. SCHENK thus implied that rising temperature is the actual cause of the start of spring migration.

STADIE (1934) described the spring migration of 1933 in Germany. First observations of woodcock were related to weather conditions, and it was possible to show agreement between rises in temperature and the arrival of the woodcock in an area.

Breeding range and winter occurrence of woodcock in Scandinavia

The woodcock occurs as a breeding bird in all Scandinavian countries. The population in Denmark was estimated to be around 1,000 breeding pairs in 1972 (CLAUSAGER 1972b). In Norway the autumn population in 1970 was estimated to be of the order of 200,000 birds, which presumably corresponds to a figure of 40–50,000 pairs (A. KRAFFT pers. comm.). The breeding population in Finland has been estimated by MERIKALLIO (1958) to be approximately 16,000 pairs. No report of the population size in Sweden is available, but numbers probably amount to many thousands.

The woodcock does not winter in Finland (SALOMONSEN 1963). In Sweden the great majority of the breeding population migrate in autumn, although along the coast of the Kattegat and in Scania the species is not uncommon in winter (HOLMSTRÖM et al. 1946). A very few woodcock regularly winter along the southern and western coasts of Norway,

and may be found as far north as the Arctic circle (HAFTORN 1971). In Denmark, woodcock remain in numbers which vary according to the severity of the winter, the majority in areas adjacent to the coast and primarily in W Jutland.

Ringing data

Up to 31 December 1971 (in Denmark 31 December 1972), 2,538 woodcock were ringed in Denmark, Norway, Sweden and Finland, and of these 327 were recovered by 31 December 1972 (by 31 December 1973 for Denmark) (Tables 1&2). More than 90 % of the birds in Norway, Sweden and Finland were ringed as pulli, as opposed to only 20 % in Denmark. The remainder of the Danish were almost

Country	No. of woodcock ringed	Period of ringing	No. of woodcock recovered	Recovered by 31. Dec.
Denmark	249	1899-1972	44	1973
Norway	331	1914-1971	35	1972
Sweden	1,079	1911-1971	145	1972
Finland	879	1915-1971	103	1972
Total	2,538		327	

Table 1. Number of woodcock ringed in Scandinavia and number of recoveries.

Cause of recovery	Country of ringing: Denmark	Norway	Sweden	Finland	Total No.	%
Shot	38	29	132	90	289	88
Found dead	2	2	10	1	15	5
Found wounded	1	–	–	–	1	–
Captured and released	2	1	–	1	4	–
Captured (no details given)	–	–	–	2	2	–
Found (no details given)	–	–	–	5	5	–
Ring found	1	–	1	–	2	–
Unknown	–	3	2	4	9	3
Total	44	35	145	103	327	

Table 3. The proportions of the different causes of recovery.

Country of recovery	Country of ringing: Denmark	Norway	Sweden	Finland	Holland	Heligoland	British Isles
Denmark	24	1	5	5	3	2	3
Norway	1	5	3	–	–	2	3
Sweden	–	–	39	–	4	5	7
Finland	–	–	–	1	1	–	–
W Germany	1	2	2	7	3	6	–
Holland	–	–	1	3	37	4	–
Belgium	–	1	5	2	7	1	–
British Isles	12	13	29	15	31	15	–
France	4	12	41	40	48	10	–
Spain	1	1	13	6	8	1	–
Portugal	–	–	2	–	1	–	–
Algeria	–	–	–	1	–	–	–
Tunisia	–	–	–	1	–	–	–
Italy	–	–	1	10	–	–	–
Yugoslavia	–	–	3	–	–	–	–
Poland	–	–	1	1	–	–	–
USSR	1	–	–	3	6	1	2
Greece	–	–	–	6	–	–	–
Turkey	–	–	–	2	–	–	–
Total	44	35	145	103	149	47	15

Table 2. Recoveries of woodcock until 31 December 1973 ringed in Denmark and until 31 December 1972 of birds ringed in Norway, Sweden and Finland. For comparison, recoveries up to 31 December 1972 are included for woodcock ringed in Holland and on Heligoland (W Germany) and for those in the British Isles later recovered in Scandinavia and the USSR.

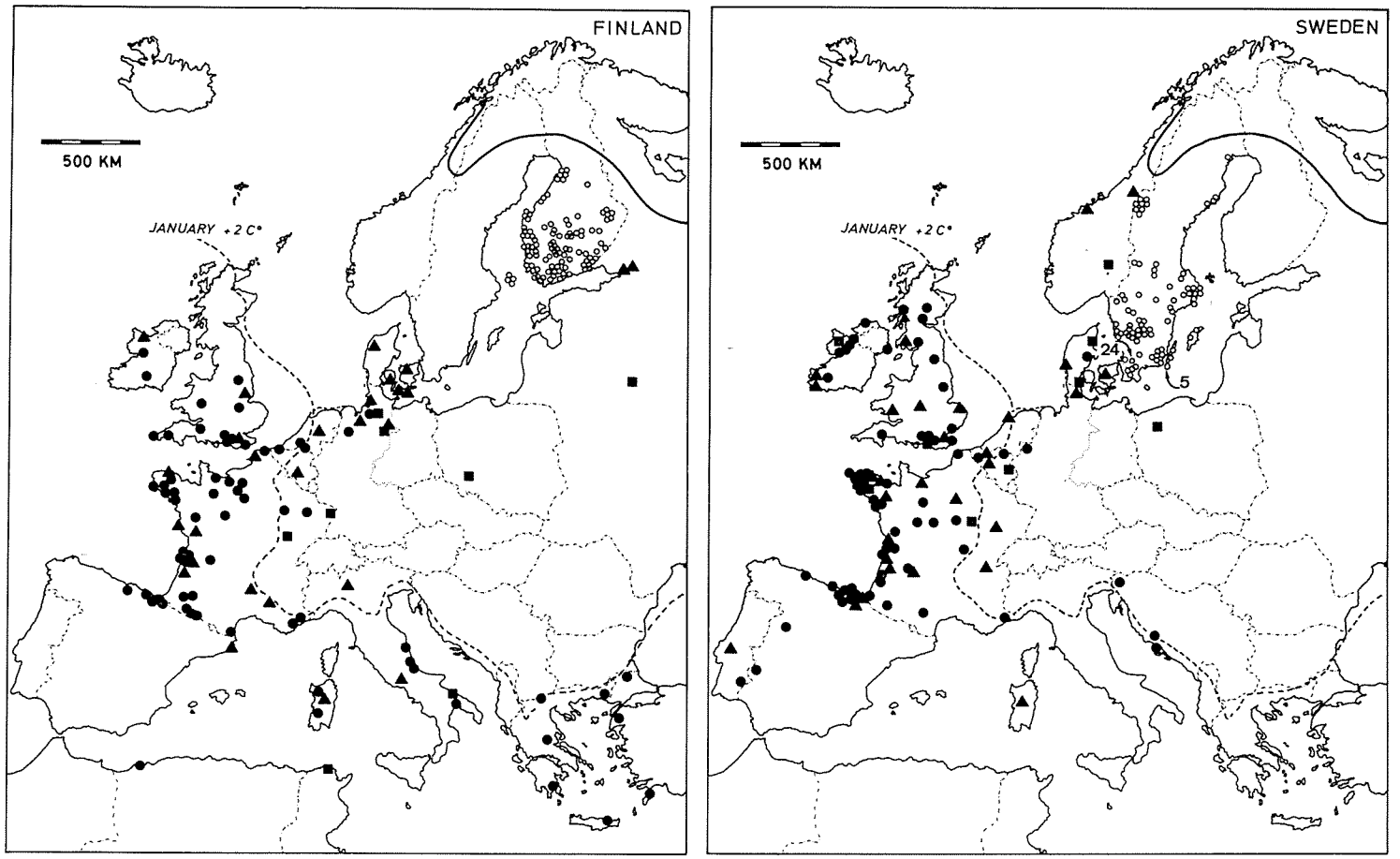

Fig. 1, see text p. 7

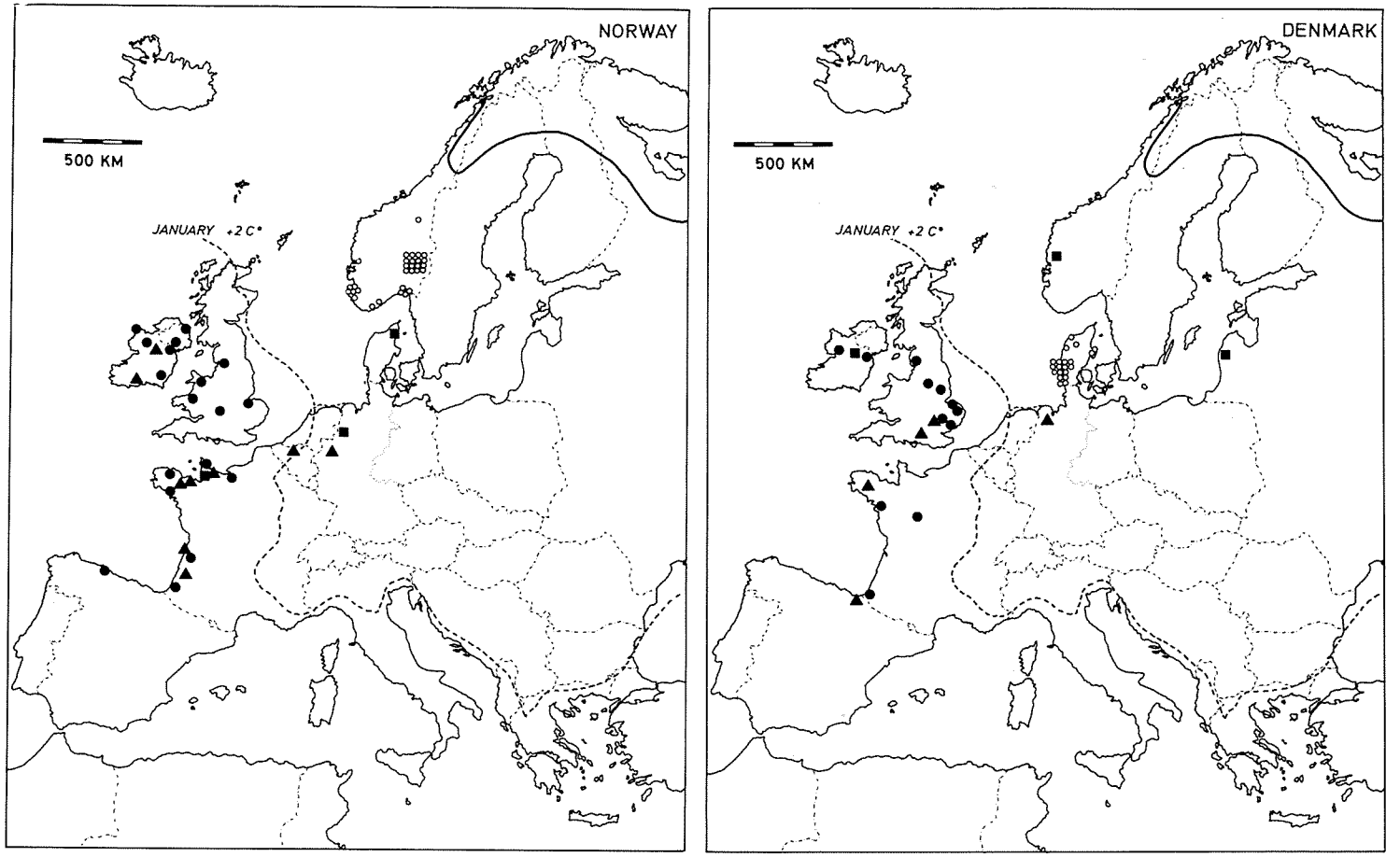

Fig. 1. Recoveries from abroad of woodcock until 31 December 1973 ringed in Denmark and until 31 December 1972 of birds ringed in Norway, Sweden and Finland. Signatures: ○ Ringing places of the recoveries. – ▲ Recovery September – November. – ● Recovery December – February. – ■ Recovery March – May. N-border of breeding range is indicated with full line, and January isotherm + 2°C with broken line.

all ringed as full-grown in the migration periods. The geographical distribution of the ringing places of the individuals recovered is shown in Fig. 1.

The causes of recovery are listed in Table 3. Excluding the cases in which the cause is unknown, the proportion of bagged birds amounts to 91 %, corresponding to the proportion found in the British Isles (BOYD 1962).

Geographical and temporal sequence of migration

FINLAND

Of the woodcock ringed in Finland, 102 were recovered abroad and one within the country. 88 were ringed as pulli and 15 as full-grown. Of the latter, 12 were ringed during the breeding season, and 3 during the spring migration.

The winter range extends from Ireland to Greece and Turkey (Tables 2 & 4 and Fig. 1). Most were wintering in France, particularly in north-western and western regions. Woodcock from Finland only reach N Africa very occasionally, and they do not appear to winter within Scandinavia, although they are recovered in N Germany in December and January.

The average direction between the place of ringing and recovery (subsequently referred to as RR-direction) is 218° during October–April. For juvenile birds the RR-direction is 220° as opposed to 217° for adults, and the difference is not statistically significant ($p>0.05$) (Table 10 p. 14).

The average distance between the place of ringing and recovery (subsequently referred to as RR-distance) is 2,300 km

Country of recovery	Month of recovery: July-Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total
Denmark	–	2	3	–	–	–	–	–	–	5
Finland	1	–	–	–	–	–	–	–	–	1
W Germany	–	1	2	1	1	–	1	1	–	7
Holland	–	–	1	2	–	–	–	–	–	3
Belgium	–	–	1	–	1	–	–	–	–	2
British Isles	–	–	3	5	4	2	–	–	–	15*)
France	–	–	8	13	12	4	2	1	–	40
Spain	–	–	1	2	1	2	–	–	–	6
Algeria	–	–	–	–	1	–	–	–	–	1
Tunisia	–	–	–	–	–	–	1	–	–	1
Italy	–	–	3	4	2	–	1	–	–	10
Poland	–	–	–	–	–	–	–	1	–	1
USSR	2	–	–	–	–	–	–	–	1	3
Greece	–	–	–	3	2	1	–	–	–	6
Turkey	–	–	–	–	1	1	–	–	–	2
Total	3	3	22	30	25	10	5	3	1	103

Table 4. Recoveries of woodcock ringed in Finland. *) Includes a recovery from Eire in "the winter" of 1968/69.

during December–February, the actual wintering period (Table 10).

Comparison of the RR-direction and RR-distance of woodcock recovered shows much variation; on average, woodcock which migrate in a more southerly direction cover greater distances than those which migrate in a more westerly direction (Table 5).

A comparison of RR-distances with January isotherms shows that the winter quarters of the woodcock lie W and S of the January isotherm of + 2° C (Fig. 1).

In Finland, woodcock begin their autumn migration in the first half of October, and the majority reach their winter quarters by the end of November. There they remain until approximately mid-March, after which a return to the breeding grounds begins to take place. The last birds do not return before well into May (Fig. 2).

RR-direction	No. of recoveries	Mean RR-distance km
171 – 210°	15	2,520
211 – 220°	12	2,450
221 – 230°	23	2,230
231 – 240°	15	2,000
241 – 270°	1	2,060
Total	66	2,300

Table 5. Mean RR-distance in relation to RR-direction for woodcock ringed in Finland and recovered during December – February.

SWEDEN

There were 145 recoveries of woodcock ringed in Sweden. Of these, 106 were from abroad, and 39 from within Sweden. Of the birds recovered, 137 were ringed as pulli, 5 as adults during the breeding season, and 3 as full-grown during the autumn migration.

The winter range extends from Ireland to Yugoslavia (Tables 2, 6 & 7 and Fig. 1). The most important winter quarters

Country of recovery	Month of recovery								
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total
Denmark	–	1	1	–	–	1	1	–	5*)
Norway	–	1	–	–	–	–	–	1	3*)
W Germany	–	1	1	–	–	–	–	–	2
Holland	–	1	–	–	–	–	–	–	1
Belgium	–	2	1	1	–	1	–	–	5
British Isles	–	8	13	5	1	2	–	–	29
France	1	11	19	5	4	2	–	–	42
Spain	–	2	5	3	2	–	–	–	12
Portugal	–	1	1	–	–	–	–	–	2
Italy	–	1	–	–	–	–	–	–	1
Yugoslavia	–	–	3	–	–	–	–	–	3
Poland	–	–	–	–	–	–	1	–	1
Total	1	29	44	14	7	6	2	1	106

Table 6. Foreign recoveries of woodcock ringed in Sweden. *) A recovery from Norway in "spring" 1927 and one from Denmark during "1957–59" are included.

are the British Isles, France and Spain, which together account for 89 % of recoveries in December–February. The average RR-direction for all foreign recoveries is 224° (Table 10). The direction for juvenile birds is calculated to 222° as opposed to 228° for adult birds. The difference is not statistically significant ($p>0.05$).

Woodcock ringed in localities north of latitude 60° N show an average RR-direction of 226° as opposed to 224° for woodcock from more southerly areas. This indicates that woodcock migrate on a broad front, explaining why birds from more northern areas winter north of the birds native to southern Sweden. A comparison of the places of recovery of the two categories also shows a clear difference; of the 19 birds ringed in the northern area and later recovered abroad, 10 (53 %) were from the British Isles and 5 (26 %) from France and the Iberian peninsula. For the 87 ringed in the more southerly area, the figures are 19 (22 %) and 49 (56 %) respectively.

Fifteen foreign recoveries of woodcock ringed in localities between 59° and 60° N indicate that the majority probably migrate E and S of the North Sea to their winter quarters, as amongst these birds only one recovery was from the British Isles (10 December in S England). The remainder were recovered as follows: Denmark 2, Belgium 1, France 9, and Spain 2. The recoveries thus indicate that woodcock breeding N of a line heading

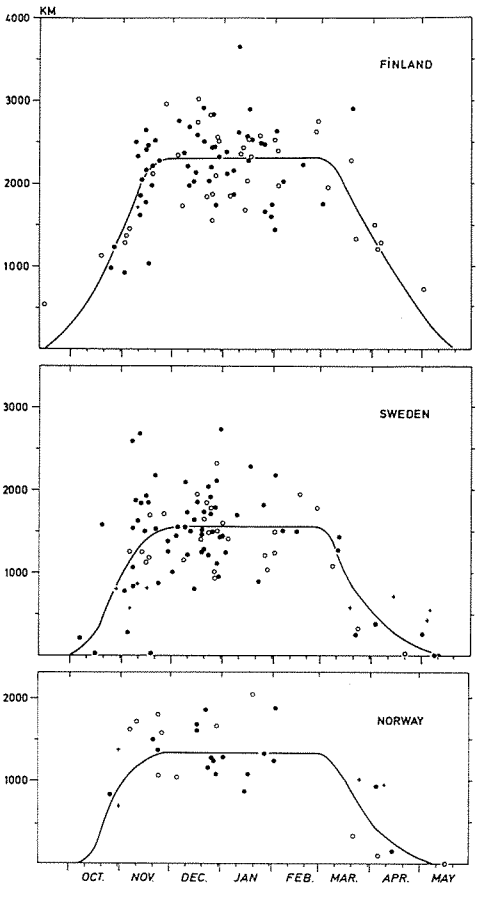

Fig. 2. RR-distance in relation to date of recovery for woodcock. Signatures: ● Recovered in the first year of life. – ○ Recovered after the first year of life. – + Date of ringing for migrants ringed in Holland, Heligoland (W Germany), the British Isles or in Denmark and later recovered in the breeding period in Finland, Sweden or Norway.

Month of recovery										
Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1	1	24	2	1	2	2	2	1	–	36

Table 7. Numbers of woodcock ringed and recovered in Sweden. Three recoveries were omitted due to lack of information.

NE from Oslo fiord mainly migrate through Norway across the North Sea to the British Isles and eventually further, while woodcock from areas S of this line generally migrate to the south of the North Sea, or cross it more southerly. Exceptions are found in both areas.

The average RR-distance for all birds recovered during the period December–February is 1,565 km (Table 10). Just as for woodcock from Finland, those from Sweden appear to cover greater distances the more southerly the RR-direction are (Table 8). Comparison of the RR-distances and the January isotherms shows that woodcock from Sweden winter S and W of the isotherm of + 2° C (Fig. 1).

The autumn migration begins in the latter half of October (Fig. 2), and the winter quarters being reached at the end of November. The return to the breeding grounds starts in the beginning of March; the first individuals are presumably back about 1 April, and the last by about 10 May. In very early springs first observations of woodcock have been done already mid-March (MARCSTRÖM 1974).

RR-direction	No. of recoveries	Mean RR-distance km
171 – 210°	6	1,380
211 – 220°	17	1,940
221 – 230°	21	1,550
231 – 240°	13	1,350
241 – 270°	8	1,280
Total	65	1,565

Table 8. Mean RR-distance in relation to RR-direction for woodcock ringed in Sweden and recovered during December – February.

NORWAY

Of woodcock ringed in Norway, 35 have been recovered; 29 were ringed as pulli, and 6 as adults or full-grown. The distribution of the recoveries is given in Tables 2 & 9 and Fig. 1.

The majority of the Norwegian population migrate to the British Isles, presumably across the North Sea, and possibly further on to the Continent. A smaller proportion appear to migrate E of the North Sea along the western coast of Jutland to their winter quarters. In spring it is possible that a larger part of the Norwegian woodcock population mi-

Country of recovery	Month of recovery									
	July	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Total
Denmark	–	–	–	–	–	–	1	–	–	1
Norway	1	1	–	–	–	–	–	2	1	5
W Germany	–	–	1	–	–	–	–	1	–	2
Belgium	–	1	–	–	–	–	–	–	–	1
British Isles	–	–	2	7	3	1	–	–	–	13
France	–	–	5	3	2	1	1	–	–	12
Spain	–	–	–	1	–	–	–	–	–	1
Total	1	2	8	11	5	2	2	3	1	35

Table 9. Recoveries of woodcock ringed in Norway.

grates E of the North Sea than in autumn after the recoveries to judge, but probably this assumption is only due to the various hunting seasons in spring in the countries around the North Sea.

During the period October–April, the mean recorded RR-direction is 224°. In December–February the mean recorded RR-distance is 1,350 km (Table 10).

The autumn migration begins about the middle of October, and winter quarters are reached by the end of November. The spring migration occurs from the beginning of March until just into May (Fig. 2).

DENMARK

Forty-four recoveries were made of woodcock ringed in Denmark. Two were ringed as pulli and 2 as adults on breeding grounds. All 4 were recovered near their ringing places in October, November, and March. It is thus not possible to state where the Danish birds winter, but it is presumed that they migrate to approximately the same regions of western Europe as the rest of the Scandinavian population. The remaining 40 birds were ringed during migration or winter as full-grown; 20 of these were recovered from abroad (Table 2 and Fig. 1).

For individuals recovered abroad during October–March, the RR-direction was 234°, and the RR-distance was 910 km. The native recoveries suggest that in Denmark, woodcock leave their breeding grounds late (2 recoveries were on 30 October and 11 November), and return to them early (recovery of 17 March).

Comparison of migration in Scandinavian woodcock

Assuming that the distribution of recoveries is representative of that of the different populations, it can be inferred that woodcock from Norway all winter in W Europe (the British Isles, France and Iberian peninsula). About 95 % of woodcock from Sweden and 75–80 % of those from Finland winter in the same area, while the remainder migrate in a southerly direction to winter quarters in Italy, the Balkan countries and Turkey.

Two-thirds of the migrants ringed in Denmark were recovered in the British Isles, and among Norwegian breeding birds almost half were recovered there; the proportions from Sweden and Finland were one-quarter and one-seventh respectively. This may be explained as follows; before woodcock arrive in Denmark, separation has taken place according to migration routes and winter quarters. The migrants which pass through Denmark are native to Sweden, Finland, the Baltic states and the north-western USSR and to a lesser extent Norway. It is presumed that some of the birds from Finland which migrate to France and Spain pass to the south of Denmark, just as those which winter in Italy and the Balkans probably pass to the east. This must also be the case for birds from the USSR, in which a separation into groups must occur, such that birds from the USSR which pass through Denmark mainly continue on to the British Isles. Recoveries of migrating and wintering

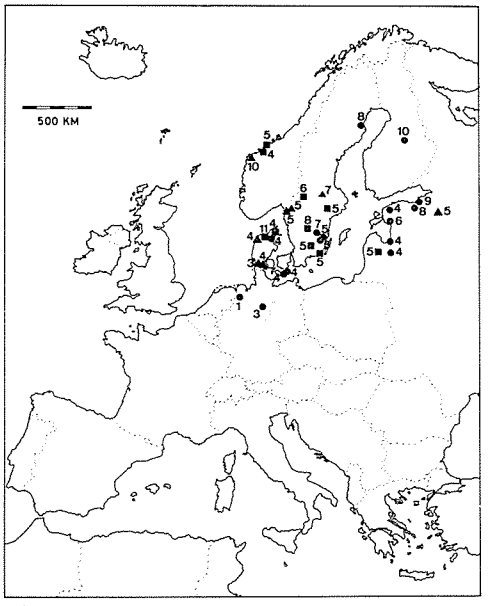

Fig. 3. Recoveries of woodcock ringed as full-grown during October–April and later recovered in countries E and N to the ringing places. The figures indicate the month of recovery. Signatures: ● Ringed in Holland. – ▲ Ringed in the British Isles. – ■ Ringed on Heligoland (W Germany).

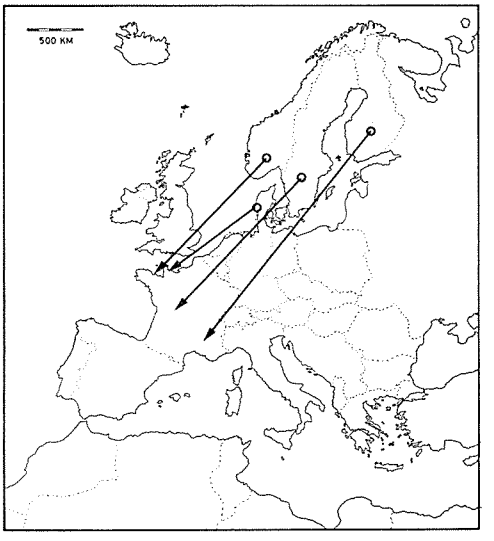

Fig. 4. Mean RR-direction and RR-distance of woodcock ringed in the Scandinavian countries.

woodcock ringed in Holland, the British Isles, Denmark and on Heligoland also confirm that parts of the winter population in W Europe consist of birds native to Scandinavia and the western part of the USSR. In Fig. 3 are shown recoveries of woodcock ringed in W Europe during October–April and later recovered mainly in the breeding period in countries N and E of the ringing places.

The country contributing most recoveries is France (Table 2). For birds ringed in Finland, only 6 % were recovered from the Iberian peninsula as opposed to 13 % of those ringed in Sweden. Only 2 woodcock were recovered in N Africa, indicating that birds from Scandinavia winter only exceptionally there.

Woodcock from Norway and Sweden have the same average RR-direction, while those from Finland migrate a little more towards the south. The migrants ringed in Denmark have on the other hand a more westerly RR-direction (Tables 10 & 11). Separation of the recoveries into monthly groups reveals no obvious changes in the RR-direction (Table 12). This implies that the migration route is relatively straight and coincident in autumn and spring.

The average RR-distance for woodcock from Finland is 2,300 km, and for those from Sweden 1,565 km. The difference corresponds exactly to the distance between the average ringing localities of the two countries. On average, woodcock from Norway do not appear to migrate as far as those from Sweden, which is presumably due to a relatively larger proportion of the former wintering in the British Isles (Table 10 and Fig. 4).

Woodcock start their autumn migration in Finland at the beginning of October, and possibly the end of September.

Country	Mean RR-direction ad.	juv.	ad. + juv.	Range	Mean RR-distance km ad.	juv.	ad. + juv.	Range
Finland	217°	220°	218°	176 – 248°	2,310	2,295	2,300	1,450 – 3,650
Sweden	228°	222°	224°	175 – 270°	1,555	1,570	1,565	650 – 2,740
Norway			224°	197 – 243°			1,350	860 – 2,030
Denmark			234°	205 – 259°			910	600 – 1,550

Table 10. Mean RR-direction and RR-distance of woodcock ringed in Scandinavian countries and recovered abroad during October – April.

RR-direction	Country of ringing: Denmark No.	%	Norway No.	%	Sweden No.	%	Finland No.	%
151 – 160°	–	–	–	–	1	1	–	–
161 – 170°	–	–	–	–	–	–	–	–
171 – 180°	–	–	–	–	2	2	6	6
181 – 190°	–	–	–	–	2	2	3	3
191 – 200°	–	–	1	6	2	2	7	7
201 – 210°	3	16	5	28	4	4	6	6
211 – 220°	3	16	2	11	32	31	18	18
221 – 230°	1	6	4	22	29	28	36	37
231 – 240°	5	28	2	11	18	18	19	19
241 – 250°	1	6	4	22	4	4	4	4
251 – 260°	5	28	–	–	5	5	–	–
261 – 270°	–	–	–	–	3	3	–	–
Total	18	100	18	100	102	100	99	100

Table 11. RR-direction of woodcock ringed in Scandinavian countries and recovered abroad during October – April.

Country of ringing	Finland		Sweden	
Month of recovery	No. of recoveries	RR-direction	No. of recoveries	RR-direction
October	3	227°	2	221°
November	20	223°	27	224°
December	29	215°	42	224°
January	25	219°	13	228°
February	10	217°	7	226°
March	5	211°	6	224°
April	3	212°	2	182°
Total	95	218°	99	224°

Table 12. Mean monthly RR-direction of woodcock ringed in Finland and Sweden.

Ring no.		Ringing and recovery data		RR-distance	RR-direction
521940	f.g.	14.01.1971	Amager: 55°38 N, 12°34 E, Denmark	185 km	250°
	+	26.03.1971	Als: 55°03 N, 09°49 E, Denmark		
T17854	f.g.	21.12.1962	Woumen: 51°00 N, 02°52 E, Belgium	390 km	249°
	×	24.01.1963	Quiberon: 47°29 N, 03°07 W, France		
T3543	f.g.	05.12.1962	Woumen: 51°00 N, 02°52 E, Belgium	590 km	228°
	+	10.01.1963	Isle of Alderney: 49°44 N, 02°13 W, Channel Islands		
1013994	f.g.	25.12.1962	De Koog: 53°06 N, 04°48 E, Holland	230 km	248°
	+	26.12.1962	Suffolk: 52°19 N, 01°35 E, Great-Britain		
1013988	f.g.	14.12.1962	De Koog: 53°06 N, 04°48 E, Holland	760 km	263°
	+	11.01.1963	Wexford: 52°18 N, 06°27 W, Eire		
584855	f.g.	17.01.1937	Heligoland: 54°11 N, 07°55 E, W Germany	520 km	203°
	+	05.04.1937	Vreese: 49°52 N, 04°56 E, Belgium		
D35331	f.g.	25.01.1926	Wesselburenkoog: 54°14 N, 08°55 E, W Germany	960 km	255°
	×	00.05.1926	Goodwick: 52°00 N, 05°00 W, Great Britain		

Table 13. Recoveries of woodcock undertaking movements in the winter period (December–February) f.g.: full-grown, +: shot, ×: found dead.

In Sweden migration can start at the beginning of October, but it does not really get under way until after mid-October, and right up to the end of November a few individuals may still be found at or near the breeding-sites. In Norway, migration starts about mid-October, but KRAFFT (1972) does point out that woodcock in the Hurdal area of S Norway appear to leave their breeding grounds before the autumn shooting starts 15 September. By the end of November almost the whole Scandinavian population has reached its winter quarters (Fig. 2).

Normally no further large movements are made from the winter quarters before the beginning of March. However, if the weather conditions worsen during the winter-period (December–February), movements may occur (Table 13). It appeared very clear in the winter 1962/63, which was severe. Four of the recoveries listed in Table 13 derive from this winter. The other three derive from winters, which were almost normal.

About the middle of March the true spring migration starts, the onset depending on the arrival of spring. In Norway woodcock return to the breeding grounds from the end of March to the beginning of May. At Hurdal the earliest arrival was 21 April (KRAFFT 1972). By 10 May in Norway, all woodcock have arrived at their breeding grounds. Similarly, birds in Sweden all appear to have returned by the beginning of May, but it is probable that those which breed furthest north return a little later. The spring migration of woodcock back to Finland takes a little longer, and it is presumed that the last birds do not return to their breeding grounds until about mid-May.

Homing and abmigration

As in other bird species, the majority of woodcock return to the places where they were hatched. ALEXANDER (1946) records that of 53 woodcock ringed as juveniles and 32 as adults in the British Isles, 45 (85 %), and 28 (88 %) respectively were recovered at or near the place of ringing. This is also the case of woodcock ringed in Sweden and recovered in the breeding period the following years (Table 14).

However, several recoveries indicate that woodcock can perform abmigration (Fig. 5). Some of the woodcock indicated on the map were recovered in March–April, and had perhaps not yet completed their spring migration. The birds recorded as bagged were probably shot on courtship flight (roding), as only this form of sport is (or was) permitted in spring in the countries from which they were recovered. According to MARCSTRÖM (1968) only males rode.

The very early beginning of egg-laying

RR-distance	No. of recoveries
0 – 1 km	7
2 – 5 km	5
6 – 10 km	4
11 – 20 km	9
21 – 30 km	4
31 – 50 km	4

Table 14. RR-distance of woodcock ringed as pulli in Sweden and recovered during April – September in following years.

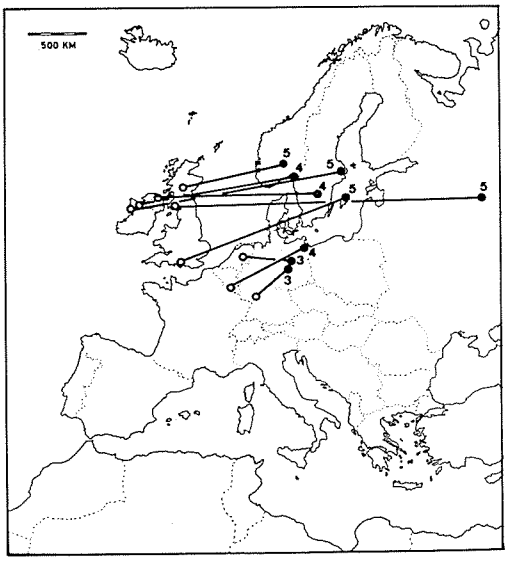

Fig. 5. Recoveries of woodcock ringed as pulli and later recovered E and N to the places, where they hatched. Signatures: O Ringing place. – ● Place of recovery (month indicated with numeral).

is indicating that pair-formation may occur before breeding grounds are reached. In this connection too, it can be mentioned that on several occasions in spring two individuals have been caught in the same trap, and this can only happen if the birds walk very close together, at a maximum distance of 30 cm. It is generally agreed that in woodcock the degree of attachment between the sexes is very slight.

Intervals of rest during migration

Several recoveries made in connection with the capture of full-grown birds on migration by the Game Biology Station illustrate how long a woodcock may rest. During the autumn, 10 birds were recovered up to 16 days after ringing at or very close to the ringing place, and in spring 2 recoveries were made 11 and 13 days respectively after ringing, at the ringing place (Table 15). The latter two should however be seen in the light of weather conditions in Denmark during spring 1970 (see p. 20). Migration can also be a very rapid event; for example, one woodcock was recovered in Spain 10 days after ringing in Denmark, the RR-distance being 1,550 km.

Sequence of migration through Denmark

A diagram of recoveries arranged according to date and distance from the ringing localities (Fig. 2), gives a general and fairly approximate picture of the temporal sequence of migration for the woodcock population of each country.

In order to study the sequence of migration through Denmark, excerpts and comparisons were made from records of woodcock bagged on various estates, where long runs of annual kills showed consistently large numbers (Figs. 7 & 8). As the Game Books consulted were kept in great detail, the material obtained may be considered as very reliable.

Date of ringing	Date of recovery	Days between ringing and recovery	Cause of recovery
24 Nov. 1969	24 Nov. 1969	0	shot
27 Oct. 1973	28 Oct. 1973	1	shot
7 Nov. 1969	8 Nov. 1969	1	shot
19 Nov. 1971	20 Nov. 1971	1	c & r
4 Nov. 1969	7 Nov. 1969	3	shot
11 Nov. 1971	14 Nov. 1971	3	c & r
15 Nov. 1971	19 Nov. 1971	4	shot
27 Oct. 1973	3 Nov. 1973	7	shot
3 Nov. 1970	10 Nov. 1970	7	shot
21 Oct. 1970	6 Nov. 1970	16	shot
27 Mar. 1970	7 Apr. 1970	11	shot
25 Mar. 1970	7 Apr. 1970	13	shot

Table 15. Woodcock recovered at or near the place of ringing. c & r = captured and released.

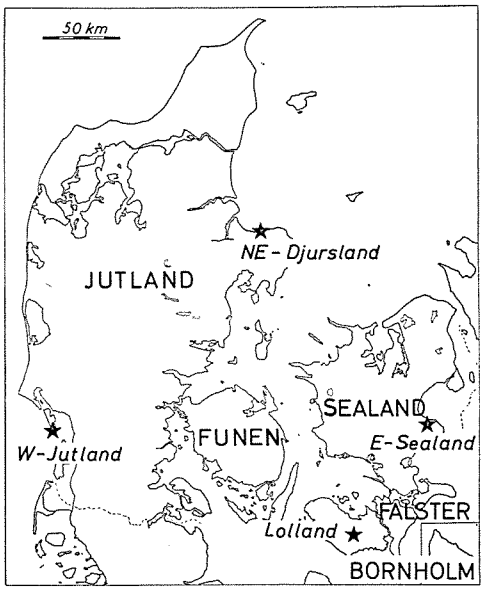

Fig. 6. Map of Denmark showing the places from where Game Books have been examined in analysing the migration of woodcock through Denmark.

THE NORMAL SPRING MIGRATION

Up to 1922 the shooting season for woodcock was 1 August–14 May, but from 1923 it was reduced to 21 September–15 April. Since the spring migration continues after 15 April, only data up to and including 1922 have been used.

The Game Books of two estates in E Sealand and NE Djursland were examined (Fig. 6). The total bag of woodcock in the two estates respectively was 2,275 individuals (1879–1922, excepting 1901–1911) and 3,430 individuals (1889–1922).

In Denmark, the spring migration of woodcock starts about 15 March, the main migration occurring during the last week of March and the first 3 weeks of April (Fig. 7). The majority of the birds bagged before 15 March are presumably wintering individuals. The last migrants occur at the end of April, although a very few (0.1 %) have been shot in early May.

Comparison of the average migration occurring at the two estates shows that spring migration occurs slightly earlier in E Jutland than in E Sealand. Furthermore, on Sealand the migration appears to be somewhat more concentrated than in Jutland. A similar difference also appears to exist between Djursland and N Jutland, although from the latter area data are only available from the period 1933–1971, during which time the open season for woodcock ended on 7 April.

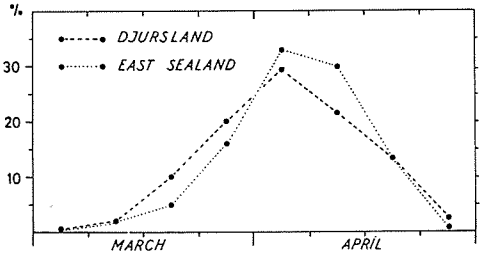

Fig. 7. Average distribution of spring migration for woodcock in NE Djursland and E Sealand.

THE NORMAL AUTUMN MIGRATION

In Denmark, the open season in autumn (since 1931 24 September–31 December) always extended over the whole of the woodcock migration period. Analyses were made of bag figures from two estates on Lolland and one on Fanø, W Jutland (Fig. 6). Bag figures from Lolland originate from the periods 1911–1970 and 1885–1967 respectively, comprising a total of 1,895 birds. The data from W Jutland comprise 2,504 woodcock bagged during 1928–1970.

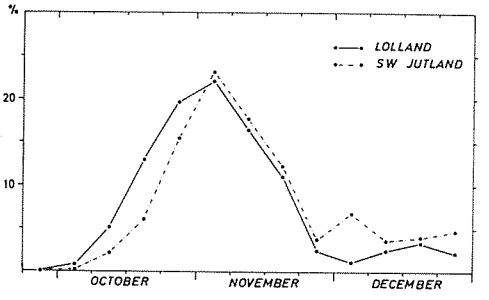

Fig. 8. Average distribution of autumn migration for woodcock in Lolland and SW Jutland.

The percentage distribution of the bag is shown in Fig. 8. In early October a few woodcock are bagged, probably birds native to Denmark which have begun to show signs of migratory activity. From the middle of the month woodcock occur in greater numbers, and the majority pass through Denmark between 20 October and 20 November approximately. The species is still frequently to be found in December, especially in W Jutland.

The autumn migration appears to reach its peak slightly earlier in the E of Denmark than in the W. This difference may be related to migration by different populations, as some of the woodcock from the Baltic states and north-western USSR pass through southern parts of Denmark.

THE SEQUENCE OF MIGRATION IN EACH YEAR, 1969–1972

Woodcock migration may vary much in time from one year to another. On the estate in NE Djursland, where the shooting pressure has been at nearly the same level all the years examined, in spring 1917 two woodcock were bagged in March, 28 during 1–7 April, and 126 subsequently. The following spring 111 birds were bagged in March, 65 during 1–7 April, and only 9 after this date. Neither the recoveries nor the bag analyses from the individual estates can give a complete picture of the occurrence of migration in a given year. For this reason, information was collected by the Game Biology Station on woodcock bagged in autumn and spring during the period 1969–1972 (Table 16).

Year	No. of bagged woodcock on which information is received		No. of bagged woodcock according to the official bag record	
	Spring	Autumn	Spring	Autumn
1969	–	3,523	8,000	19,000
1970	2,978	2,347	9,000	17,000
1971	2,117	1,485	4,000	14,000
1972	966	–	3,000	13,000

Table 16. The number of woodcock on which information was received compared with the figures from the official Danish bag record.

Autumn 1969

Woodcock arrived late in Denmark in the autumn of 1969 (Fig. 9), due to the very mild weather prevailing in October in regions E and NE of Denmark. Only a few birds were bagged before 20 October, and most of these presumably were birds which had bred in Denmark, as the majority were bagged at or in the vicinity of woodcock breeding grounds.

In the SE regions of Denmark (particularly Bornholm, Lolland and Falster), many woodcock were present around 25 October; this migration only affected Jutland to a small extent in its southern parts. Information indicates that the woodcock actually arrived on 24 October, but intensive shooting first began on the 25th which was a Saturday.

On 6 November and days immediately following, large numbers of woodcock were in evidence, particularly in W and S Jutland. This influx only affected the islands to a small extent. No large concentrations occurred later in the shooting season. During the last week of November the temperature dropped to below zero, and almost all woodcock disappeared. As a result, in December only 3.5 % of the total autumn bag were taken, as opposed to the more normal value of 10 % in this month.

Autumn 1970

The migration of 1970 also began rather late, as the first observations of large numbers of birds were made on 1 November (Fig. 9), particularly in N Jutland and the islands, while in W and S Jutland the woodcock did not arrive until the next day. The difference in occurrence was undoubtedly due to a warm front which moved NE over Jutland on the night of 31 October–1 November, accompanied by rain and low visibility; this caused the birds to interrupt their migration. After 1 November the weather was very mild up to the end of the year, and consequently the migration faded out only gradually.

Autumn 1971

Migration began very early in 1971 (Fig. 9). The first woodcock were observed on 16 October, a Saturday, in W Jutland. However, the weather situation indicated that these birds had arrived one or two days earlier, but sportsmen were not active until Saturday.

The next influx occurred on 24 October in the islands, and 26 October in SW Jutland. In this latter area the woodcock continued on their journey already the following night, and during the next days there were very few woodcock in Denmark. They began to appear again about 6 November, but larger numbers were not observed until 10 November.

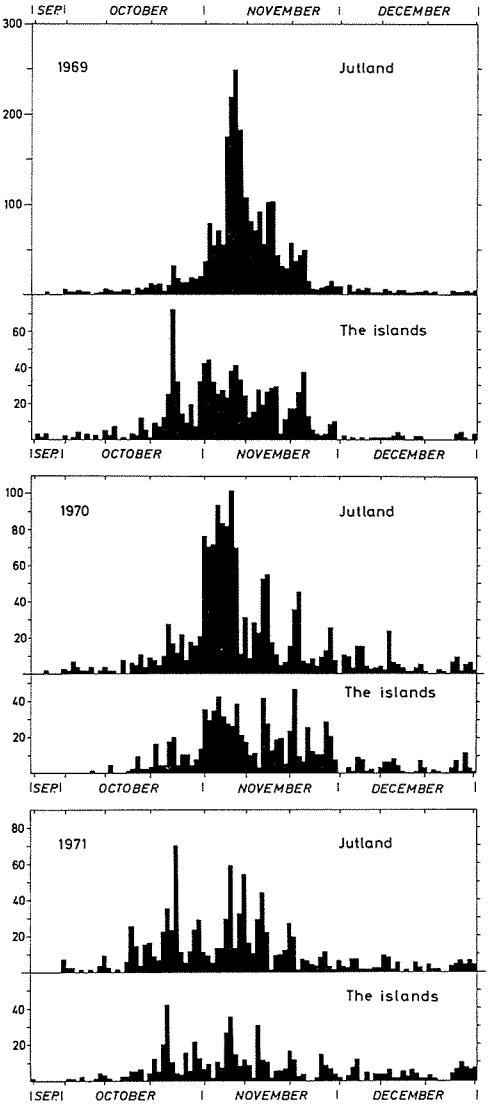

Fig. 9. Autumn migration of woodcock in Denmark in 1969, 1970 and 1971. The distributions are based on woodcock bagged. The figures left indicate numbers of woodcock of which information was received. "The islands" comprise the islands E of the Lillebælt.

On 21 November many woodcock left Denmark as a result of a violent blizzard, but the snow disappeared fairly rapidly, and the weather for the remainder of the year was very mild. Thus even although many woodcock had migrated through Denmark a considerable proportion still remained, and in December 12 % of the total bag was taken.

The autumn migration, 1969–1971

In the three years described above the occurrence of the autumn migration showed great variation with regard to onset, culmination, and termination (Fig. 9). Reports of occurrence were nevertheless in very good agreement with the ringing results (Fig. 2). The actual autumn migration begins about mid-October, and the majority of the woodcock reach their winter quarters around 20 November. The relatively large bag numbers in December are unusual, as no recoveries were made in Denmark of birds from either Sweden or Finland during this month. However, one Swedish woodcock, which were recovered in Denmark, had no exact date of recovery, only the date of the reporting letter to 31 December.

Spring 1970

The spring migration began late after the prolonged winter of 1969/70, and out of 2,978 woodcock only 13 were bagged during the period 1–21 March (Fig. 10). The first woodcock from abroad arrived about 22 March, but intensive woodcock shooting did not begin until 26 March, (Maundy Thursday), a public holiday. Denmark was still completely covered by snow, and thus the birds did not continue on their migration, but remained in the country for several days. As the weather situation did not change until after 7 April, there was a constant accumulation of newly-arrived woodcock, see Fig. 10.

After 7 April the information was more scanty, but in many places the woodcock still remained about a dozen days. However, there was nothing to indicate that conclusion of the migration was delayed.

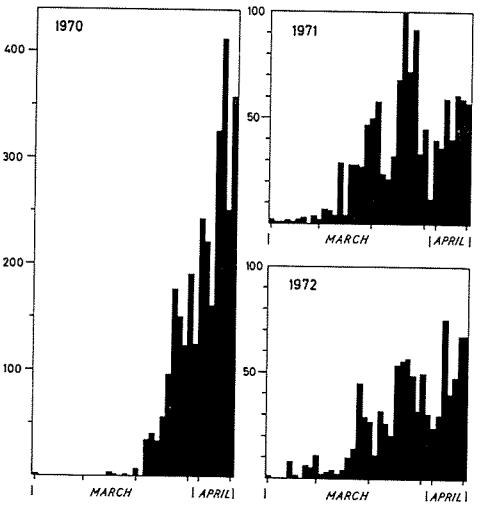

Fig. 10. Spring migration of woodcock in Denmark until 7 April in 1970, 1971 and 1972. The distributions are based on woodcock bagged. The figures left indicate numbers of birds of which information was received.

Spring 1971

In 1971, spring arrived very early. Until 25 February the winter was very mild, and as early as 20–25 February woodcock were observed at several places, being presumably forerunners of the spring migration. Due to a cold spell with NE winds from 25 February until the beginning of March, the early spring migration was discontinued (Fig. 10), and very few birds were bagged before 10 March. On 14 March a fair number of woodcock were bagged, and in the following fortnight the weather was mild and changeable with SW winds. Birds arrived almost daily from abroad, but not in large concentrations on any given day. Furthermore, the woodcock rapidly continued on their journey. At the end of March and beginning of April the wind alternated between NE and SE, and the weather was rather cold with night temperatures of below freezing. Thus no appreciable numbers of woodcock arrived in Denmark during the last few days of the shooting season. After 7 April as in spring 1970 only few records of birds were received.

Spring 1972

In Denmark, the winter of 1971/72 was not particularly severe. In March the wind was mainly in the E until about the 20th, when

it changed to the W and remained there until the first part of April. The spring migration began relatively early. The distribution (Fig. 10) indicates that there was a small influx in early March, but the migration was only considerable after about 15–20 March. Due to the mild weather the migration was dispersed without days of large concentrations, and in general the spring migration was earlier than usual.

The spring migration, 1970–1972

Although the data do not cover the whole of the spring migration period, the graphs (Fig. 10) provide a clear impression of the way in which woodcock migration can vary from one year to another. In particular it is the start of migration which changes, influenced by the arrival of spring, while its conclusion appears to be much less variable. In a very early spring, the first migrants may arrive in Denmark as early as the end of February, but it is more usual for them to arrive about mid-March, and in late springs arrival may be delayed even until the end of this month.

The influence of weather on migration

As mentioned previously (p. 5), several authors have attempted to determine which factors affect migration itself. The majority appear to be agreed on the importance of temperature in this respect.

Woodcock migrate at night and rest during the day. The flight begins at dusk and unless the birds are forced to stop flying by unfavourable weather such as rain or mist, they continue until dawn. Both in spring and autumn, woodcock are able to fly in the dark for 10–12 hours per night. Depending on wind conditions their flight speed of 40–50 km/hour enables them to cover 400–600 km in a single night.

In autumn, woodcock arriving in Denmark would have set off the previous evening from southern or central Sweden or the Baltic states, while in spring they would have come from Holland and Belgium, or SE England (Fig. 11). Thus in analysing the possible connections between weather conditions and migration, it is natural to consider the weather conditions applying in regions where woodcock might be expected to set off the evening before arriving in Denmark.

The distribution of figures for bagged woodcock (Figs. 9 & 10) which formed the basis of the analyses were very useful in the case of autumn migration, as numbers were sufficiently large and were obtained throughout the whole migration

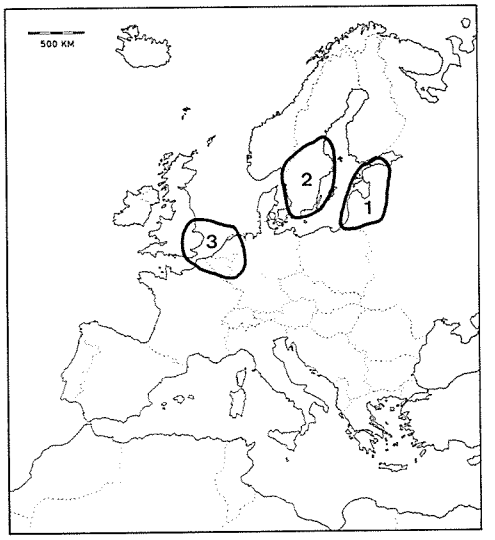

Fig. 11. Areas from which the woodcock likely set off the evening before they arrive in Denmark. 1 and 2: Starting areas in autumn. – 3: Starting area in spring.

period. This was only true to a lesser extent in the case of the spring migration, as the relevant graphs only cover a portion of the migration period. Furthermore the spring migration of 1970 was very abnormal, as after their arrival in Denmark, the woodcock remained until after the end of the shooting season on 7 April. The spring migrations in 1971 and 1972 were small, and bag records show no large numbers on any day.

Other factors regularly influence graphs of this kind and some of the more important of these are described briefly below:

The amount of shooting (shooting pressure) is not the same every day of the week; calculations show that it is about twice as great on Saturdays, Sundays and public holidays as on ordinary week-days.

Poor weather conditions such as rain, snow, high winds, etc., reduce the sportsman's desire to go shooting. In the graphs shown, days on which few woodcock were bagged in relation to previous and subsequent days were often days on which the weather was poor. Precipitation in particular is an important factor here.

Woodcock interrupt their migration for shorter or longer periods, and thus a large bag on a particular day does not necessarily indicate a large influx of woodcock the previous night. On the other hand, changes in the daily bag numbers can indicate whether woodcock arrived the previous night or not.

Bearing these factors in mind, it was possible to select the days listed in Tables 17 & 18, on which very many woodcock were recorded, from the graphs of Figs. 9 & 10. The days listed do not include all days with large numbers of woodcock, but from the graphs it could be deduced that woodcock had arrived at least in the days immediately before those listed. In order to determine whether changes in weather conditions were of the same character every time, meteorological data were compared from days on which large changes in bag numbers were recorded. Weather reports and maps from 00°° Greenwich Mean Time produced by the Meteorological Institute, Copenhagen, were used for this purpose (see Tables 17 & 18).

It is seen from Fig. 9 that many woodcock were bagged in the islands on 25 October. However, the indications are that the birds arrived the previous day, but they were not a sought-after item of sport until the next day, a Saturday.

Weather maps show that the temperature in the Baltic states fell from 6.8° C on the night of the 22–23 October to 0.2° C on the night of the 23–24. In southern and central Sweden, the temperatures on the corresponding nights were 3.0° C and 4.5° C. The drop in temperature in the Baltic states was accompanied by partial clearing of cloud cover and a light ESE wind. In Sweden, the sky was overcast both nights and the wind light E. The barometric pressure rose 7 mb in the Baltic states, while it fell 6 mb in Sweden.

The arrival of woodcock was restricted to SE Denmark (Bornholm and Lolland-Falster), and it can be assumed that the birds came from the Baltic states. If they had come from southern Sweden, woodcock would also have been recorded in Jutland, as there were no adverse weather conditions to prevent this. A similar description to that of 24 October 1969 can be applied to the remaining days listed in Tables 17 & 18.

In autumn, there was a considerable drop in temperature during the evening in regions where woodcock set off for Denmark to arrive the next day. The drop in temperature was accompanied by partial or complete clearing of cloud cover, decreasing wind speed to light breeze or less, and a rise in barometric pressure of 7–20 mb during the foregoing 24 hours. Which factor or combination of factors causes the release of the migratory impulse is open to discussion, but there can scarcely be any doubt that one of these factors, either alone or in conjunction with others, is responsible for the migratory impulse of woodcock.

At the end of November 1969, there

	Baltic states					Southern and Central Sweden			
Date	Occurrence of woodcock in Denmark	Temperature change during previous night °C	Cloud cover	Wind speed and direction	Change in barometric pressure mb	Temperature change during previous night °C	Cloud cover	Wind speed and direction	Change in barometric pressure mb
24 Oct. 1969	Bornholm Lolland-Falster	6.8 → 0.2	partially clearing	light, E – SE	+ 7	3.0 → 4.5	overcast	light, E – SE	÷ 6
6 Nov. 1969	Jutland	4.6 → 1.0	overcast	light, W	+ 18	2.8 → ÷4.5	clearing	calm	+ 20
1 Nov. 1970	N and NW Jutland	9.5 → 5.3	overcast	almost calm	+ 20	3.5 → ÷4.0	clearing	calm	+ 15
26 Oct. 1971	SW Jutland	10.3 → 7.0	50% overcast	light to moderate, NW	+ 8	9.0 → 1.0	clearing	light, variable	+ 18
10 Nov. 1971	W Jutland	6.8 → 3.8	overcast	light, variable	+ 5	2.0 → ÷5.0	clearing	calm	+ 20

Table 17. Meteorological data for days on which larger numbers of woodcock were noted in autumn in Denmark.

	Holland, Belgium and SE England			
Date of arrival of woodcock in Denmark	Temperature change during previous night °C	Cloud cover	Wind speed and direction	Change in barometric pressure mb
22 March 1970	7.0 → 8.0	Overcast	light, SW	÷ 5
27 March 1970	0.0 → 3.0	Overcast	light, W-NW	÷ 10
30 March 1970	2.0 → 6.0	Overcast	light, SW	÷ 2
13 March 1971	2.0 → 5.0	Overcast	light, SW	÷ 7
25 March 1971	5.0 → 8.1	Overcast	light, SW	÷ 5
3 April 1972	9.0 → 10.8	Overcast	fresh, W	÷ 5

Table 18. Meteorological data for days on which larger numbers of woodcock were noted in spring in Denmark.

was a drop in temperature in most countries including Denmark. The average temperatures at the Meteorological Institute, Copenhagen, for 23, 24 and 25 November were 3.1°, –0.3°, and –2.0° C respectively. During the night of 23–24 November cloud cover partially cleared, and the wind was light and changeable. The barometric pressure fell gradually by a total of 17 mb from early morning on 22 November until afternoon on 24 November. The very great majority of woodcock set off on the night of 23–24 November (Fig. 9), that is to say, during a period of falling barometric pressure. Changes in this factor are thus not likely to be the direct cause of the initiation of the migratory impulse in autumn.

In the case of the spring migration, the data presented in Table 18 show a similar obvious connection between changes in weather conditions and numbers of woodcock. In each case, there was a rise in temperature in the probable region from which the birds departed. Furthermore the sky was overcast, the wind light to moderate between S and W, and the barometric pressure generally falling.

To summarize, it can be concluded that the arrival of woodcock in Denmark in autumn is closely connected with a marked drop in temperature immediately beforehand in areas NE and E of the country. In the spring, a rise in temperature in areas SW of Denmark initiates the migration. The analyses show that temperature changes in spring do not need to be as large as those in autumn to initiate the migratory impulse.

Age distribution of migrating birds

Primaries were collected from bagged woodcock from autumn 1970 until spring 1972. It is possible to determine whether a feather is from an adult or juvenile bird by the degree of wear (CLAUSAGER 1973a).

The geographical distribution of primaries collected is given in Table 19. The juvenile:adult ratio in 1970 was 2.5:1 as opposed to 2.7:1 in 1971. If the figures are corrected so that regional percentage distributions are the same each year, the juvenile:adult ratio becomes 2.64:1 in 1970 and 2.72:1 in 1971. This gives no reason for believing that there was a difference in the breeding success of these two years.

The temporal distribution of woodcock (Table 20 and Fig. 12) illustrates that the

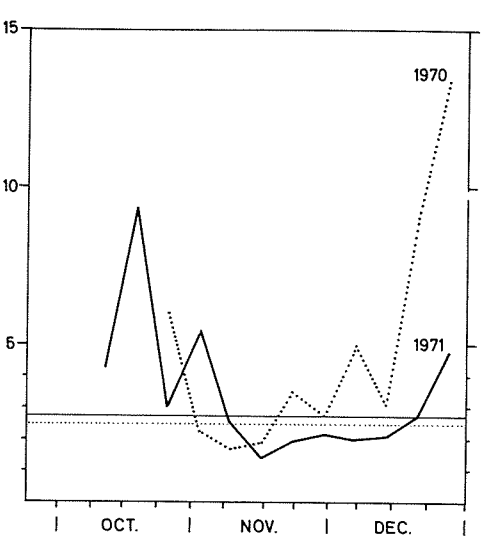

Fig. 12. Juvenile: adult ratios of woodcock bagged in Denmark during the autumn 1970 and 1971. Mean values are indicated by horizontal lines.

Region	1970 ad.	1970 juv.	1970 juv. %	1970 juv./ad. ratio	1971 ad.	1971 juv.	1971 juv. %	1971 juv./ad. ratio
Islands	54	180	76.9	3.3	65	212	76.5	3.3
N Jutland	59	142	70.6	2.4	44	123	73.6	2.8
E Jutland	40	85	68.0	2.1	21	50	70.4	2.4
S and W Jutland	131	316	70.7	2.4	120	297	71.2	2.5
Jutland total	230	543	70.2	2.4	185	470	71.8	2.5
Denmark total	284	723	71.8	2.5	250	682	73.2	2.7

Table 19. The geographical distribution of woodcock bagged in autumn 1970 and 1971, from which primary feathers were obtained.

Bagged during	1970 ad. %	1970 juv. %	1971 ad. %	1971 juv. %	1970 1971 juv.:ad. ratio	
24–30 Sept.	–	–	–	–	–	–
1–7 Oct.	–	0.1	–	0.8	–*)	–*)
8–14 Oct.	0.4	0.4	0.9	1.6	3.0	4.3
15–21 Oct.	–	3.2	3.1	9.7	–*)	9.4
22–28 Oct.	3.3	8.0	18.8	21.4	6.1	3.0
29 Oct.–4 Nov.	30.0	26.7	5.7	11.7	2.3	5.5
5–11 Nov.	31.9	21.0	23.1	22.0	1.7	2.6
12–18 Nov.	14.4	10.8	19.6	10.2	1.9	1.4
19–25 Nov.	7.8	10.9	12.6	8.5	3.6	1.9
26 Nov.–2 Dec.	5.9	6.4	4.8	3.3	2.8	2.2
3–9 Dec.	2.6	4.1	3.1	2.0	4.0	2.0
10–16 Dec.	2.6	3.2	3.5	2.7	3.1	2.1
17–23 Dec.	0.4	1.3	2.6	2.5	9.0	2.8
24–31 Dec.	0.7	3.9	2.2	3.6	13.5	4.8
24 Sept.–31 Dec.	100.0	100.0	100.0	100.0	2.5	2.7

Table 20. The temporal distribution of adult and juvenile woodcock in autumn 1970 and 1971, from which primary feathers were received.
*) no feathers from adult birds during this period.

Region	Bagged 1 March – 7 April 1971 ad.	juv.	juv. %	juv.: ad.	Bagged 1 March – 7 April 1972 ad.	juv.	juv. %	juv.: ad.
Islands	114	135	54.2	1.2	91	100	52.4	1.1
N Jutland	108	107	49.8	1.0	137	94	40.7	0.7
E Jutland	79	71	47.3	0.9	91	68	42.8	0.7
S and W Jutland	42	32	43.2	0.8	45	39	46.4	0.9
Jutland total	229	210	47.8	0.9	273	201	42.4	0.7
Denmark total	343	345	50.1	1.0	364	301	45.3	0.8

Table 21. The geographical distribution of woodcock bagged in spring 1971 and 1972, from which primary feathers were obtained.

Bagged during	1971 ad. %	1971 juv. %	1971 juv.: ad. ratio	1972 ad. %	1972 juv. %	1972 juv.: ad. ratio
1–5 March	–	0.6	–*)	0.8	1.3	(1.6)
6–10 March	–	1.3	–*)	3.0	1.7	(0.9)
11–15 March	3.7	4.1	(1.1)	1.1	2.4	(2.2)
16–20 March	16.5	17.4	1.0	15.0	10.1	0.6
21–25 March	17.1	17.1	1.0	18.0	12.7	0.6
26–30 March	31.8	28.2	0.8	27.6	25.2	0.7
31 March – 3 April	11.2	13.0	1.2	20.0	18.1	0.7
4–7 April	19.7	18.3	0.9	14.5	28.5	1.6
1 March – 7 April	100.0	100.0	1.0	100.0	100.0	0.8

Table 22. The temporal distribution of adult and juvenile woodcock in spring 1971 and 1972, from which primary feathers were received.
*) no feathers from adult birds in this period.

migration of adult birds is more concentrated than that of juveniles. In 1970, 90 % of adults bagged were taken between 29 October and 2 December, as opposed to 76 % of juveniles. In 1971, 85 % of adults were bagged during 22 October–2 December in contrast to 77 % of juveniles. χ^2-tests showed that these differences between the times of adult and juvenile migration were significant ($p<0.001$).

It is noticeable that the juvenile:adult ratio at the end of December is much greater than the average value for the whole of autumn. It suggests that the majority of woodcock which winter in Denmark are juveniles, and this is borne out by specimens at the Zoological Museum, Copenhagen; in the collection there is only one adult bird from January–February as opposed to 10 juveniles from the same period.

SPRING

The geographical distribution of primaries collected is given in Table 21. The material separated into adult and juvenile categories, the latter group consisting of birds hatched in the previous breeding season.

In 1971, the juvenile:adult ratio during the period 1 March–7 April was 1.0:1 as opposed to 0.8:1 in 1972. The considerably smaller ratio in spring in comparison to that in autumn may be partly due to the fact that juvenile birds are probably bagged more easily than adult birds in autumn, thus giving a higher juvenile:adult ratio than is actually the case. This is scarcely so in spring. In addition, if in autumn juveniles are more easily bagged than adults, this would result in a progressive reduction of the juvenile:adult ratio.

The data from the material (Table 22 and Fig. 13) only give a slight indication that migration of juveniles in spring is later than that of adults, but as mentioned later (p. 28), a distinct difference can be seen when the material is divided into categories of sex and age.

Sex ratio during migration

Woodcock specimens, for which the exact details of date and locality where bagged were known, were used for an analysis of the sex composition of migrating birds. The sex of each individual bird was determined by examination of the gonads. Specimens of sex-determined woodcock from the Zoological Museum, Copenhagen, and the Game Biology Station, were also included in the analysis.

The investigation showed that the sex composition of the material depended upon the time of its collection. Furthermore, the type of shooting practised is an important factor, and in spring it may definitely introduce a systematic source of error into the material. Various sex compositions are given by McCabe & Brackbill (1973), but these are of questionable value without the dates of collection and without knowing the type of shooting employed.

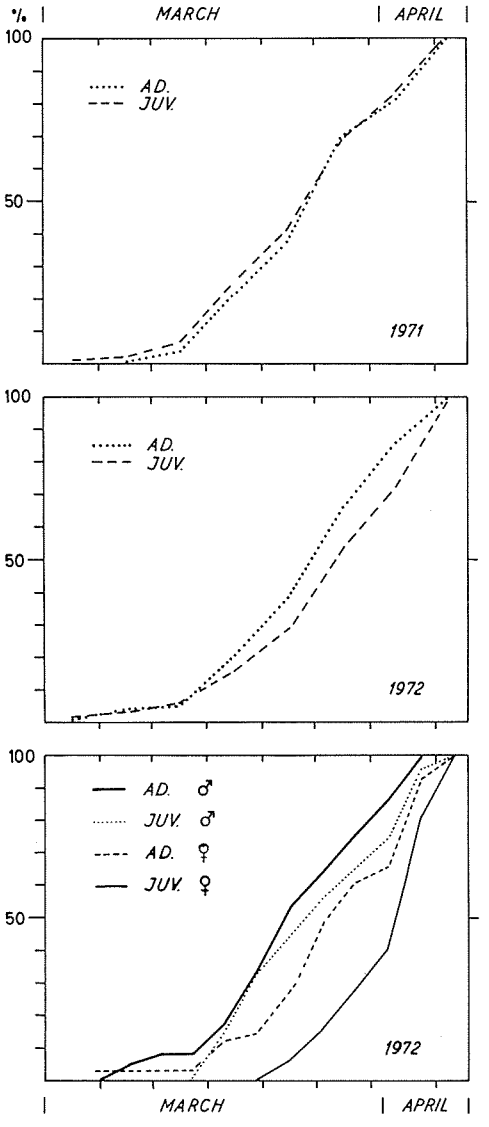

Fig. 13. Cumulative distribution of spring migrants in Denmark until 7 April of adult and juvenile woodcock in 1971 and 1972. The lowest diagram shows the distribution of 175 aged and sexed woodcock bagged in spring 1972 (see also Table 25).

AUTUMN

The material used comprises 101 individuals shot in the period 24 September–31 December in the years 1969–1971, and 69 museum specimens, which nearly all were bagged or killed at lighthouses (1895–1957). A total of 14 individuals from January–February were also considered.

It is evident from Table 23 that males and females are equally represented amongst both juvenile and adult woodcock. As the composition of the material is much the same as that of the average autumn migration, it can be presumed from the sex composition of the material described above that the woodcock population has a sex ratio of 1:1. McCabe & Brackbill (1973) concluded that the male:female ratio was 54:46 (i.e. 1.17:1), but as mentioned previously the time of collection and type of shooting employed may affect the results.

SPRING

In spring 1970, 1971 and 1972, a total of 279 bagged woodcock were obtained (Table 24). Spring hunting employed in Denmark has always been on birds flushed up, never on individuals on courtship flight. As mentioned on p. 21, the onset of spring migration varies considerably from one year to another, and thus it is not possible to group data from several years together as was done for the autumn migration, if the sex distribution is to be satisfactorily examined.

In all three years, the sex distribution is such that there were more males at the start of migration, while females were in the majority towards the end of the open season for woodcock.

The separation of the material into adult and juvenile categories (p. 26) revealed only a slight difference during the

Period	ad. ♂	juv. ♂	Total ♂♂	ad. ♀	juv. ♀	Total ♀♀	Total
21–31 Sept.	–	1	1	–	–	–	1
1–10 Oct.	–	3	3	1	9	10	13
11–20 Oct.	–	–	–	–	6	6	6
21–30 Oct.	6	11	17	5	10	15	32
1–10 Nov.	11	19	30	12	13	25	55
11–20 Nov.	8	2	10	7	4	11	21
21–30 Nov.	6	6	12	2	4	6	18
1–10 Dec.	–	4	4	4	5	9	13
11–20 Dec.	2	5	7	2	–	2	9
21–31 Dec.	–	1	1	1	–	1	2
21 Sept. – 31 Dec.	33	52	85	34	51	85	170
1–10 Jan.	–	4	4	–	1	1	5
11–20 Jan.	1	1	2	–	2	2	4
21–31 Jan.	–	1	1	–	–	–	1
1–10 Feb.	1	1	2	–	2	2	4
1 Jan. – 10 Feb.	2	7	9	–	5	5	14

Table 23. The temporal distribution of woodcock determined as to sex and age.

temporal sequence of the spring migration, and the same is true in the case of 175 sex- and age-determined woodcock from 1972. The age distribution of these birds at various times was comparable to that of the total material for this year (Table 22 and Fig. 13). However, a further separation into age and sex categories revealed distinct differences in the sequence of migration. Adult males migrate first, followed by juvenile males, which migrate a little earlier than adult females, and finally the juvenile females arrive (Table 25 and Fig. 13).

	1970		1971		1972	
	Sex					
Period	♂	♀	♂	♀	♂	♀
1–7 March	–	–	–	–	–	1
8–15 March	–	–	1	–	5	–
16–23 March	–	–	9	1	41	12
24–31 March	19	6	21	15	32	24
1–7 April	3	8	13	8	24	36
Total	22	14	44	24	102	73

Table 24. The sex distribution of woodcock bagged in spring 1970–1972.

	Sex and age				
Period	ad. ♂	ad. ♀	juv. ♂	juv. ♀	Total
1–3 March	–	–	–	–	–
4–6 March	–	1	–	–	1
7–9 March	3	–	–	–	3
10–12 March	2	–	–	–	2
13–15 March	–	–	–	–	–
16–18 March	6	4	6	–	16
19–21 March	9	1	8	–	18
22–24 March	12	5	5	2	24
25–27 March	6	9	5	3	23
28–30 March	7	5	4	4	20
31 March – 2 April	6	2	4	4	16
3–5 April	8	11	9	13	41
6–7 April	–	3	2	6	11
Total	59	41	43	32	175

Table 25. The temporal distribution of woodcock determined as to age and sex, bagged during spring 1972.

Mortality and population turnover

The mean annual mortality rate was calculated from recovery data on woodcock ringed as pulli before 31 December 1967. As Scandinavian woodcock can be generally said to share the same winter quarters, and have the same migration routes, it is presumed that the mortality factors to which they are subjected are much the

same. For this reason, recoveries from each country were grouped together (Table 26), and in any case, a χ^2-test revealed no significant difference ($p > 0.05$) in the temporal distribution of recoveries when the data for each country were treated separately.

The transitional date between age-groups was chosen as 1 August. Young birds were thus classified as first-year olds if they were recovered before 1 August of the following year. The transition date is such that in almost all cases the dates of ringing are prior to it, and thus for most of the birds the first year becomes more than 12 months.

During the first year of life, recorded mortality is higher than in subsequent years; out of a total of 227 woodcock, 149 (65.6 %) were recovered before the end of the first year of life. If the mean annual mortality for adult woodcock is presumed to be the same for all subsequent age-classes, it would have a value of 50.6 ± 4.0 %. Considering the relatively small number of recoveries, this figure must be treated with some caution.

In Holland, a number of woodcock have been ringed on the autumn migration (Table 26); as shown earlier, the great majority of these come from Scandinavian countries. The ringed woodcock were not of known age, and it was thus impossible to calculate a mortality rate for the first year of life. The mean annual mortality of adult woodcock (i.e. those recovered more than one year after ringing) was calculated to be $50.0\ \% \pm 5.6\ \%$, corresponding very closely to the mortality rate found for woodcock in Scandinavia. The mean annual mortality rate for migrants ringed on Heligoland in autumn appears to be of the same order, but the data were insufficient for calculations.

Comparison of the mortality rate among woodcock in Scandinavia with that in the British Isles (Table 27) shows considerably greater mortality in Scandinavian birds. The difference is mainly to be found in the fact that woodcock in Britain and Ireland are chiefly sedentary birds, whereas these of Scandinavia are almost exclusively migrants. Migration

Age in years	No. of recoveries of woodcock ringed in				Total	Years after ringing	No. of recoveries of woodcock ringed in Holland
	Denmark	Norway	Sweden	Finland			
1	–	13	91	45	149	1	55
2	1	6	24	13	44	2	21
3	1	–	9	6	16	3	10
4	–	1	3	3	7	4	3
5	–	1	2	2	5	5	2
6	–	–	2	1	3	6	1
7	–	–	1	–	1	7	1
8	–	–	–	–	–	8	–
9	–	1	–	1	2	9	–
10	–	–	–	–	–	10	1
Total	2	22	132	71	227		94

Table 26. The temporal distribution of recoveries of woodcock ringed as pulli in Denmark, Norway, Sweden and Finland until 31 December 1967, and recoveries of birds ringed in Holland during October – April until 31 December 1967.

exposes birds to a greater mortality risk, and thus the mean annual mortality rate is increased. Another factor of possible importance is that a considerable proportion of Scandinavian birds are exposed to shooting for a longer period than birds in Britain and Ireland, because several of the countries through which they pass during migration have a longer open season than the British Isles, and some allow shooting in spring.

The mean mortality rate for first-year birds is 65.6 %, and 50.6 % for older age-groups. Thus the mean life expectancy for juvenile woodcock is approximately 14 months, as opposed to almost 18 months for older birds.

The mortality rate for first-year birds corresponds well with the age distribution found in the autumn bag of woodcock in Denmark. Here the percentage of juveniles in 1970 and 1971 was 71.8 % and 73.6 % respectively (Table 18), sligthly larger than the calculated mortality rate. This is to be expected for several reasons, as in autumn Denmark is the first country in which woodcock from Sweden and Finland are exposed to a considerable amount of shooting; and the migrants found in Denmark belong to a population previously more or less unaffected by shooting. For instance, in Finland only a few hundred birds are bagged annually (RAJALA pers. comm.), while the bag in Sweden is a few thousand (MARCSTRÖM pers. comm.). Therefore when the migrants arrive in Denmark in October–November the juvenile:adult ratio will be greater than at any other later time. In addition, juveniles at this time of year are inexperienced and therefore easier to shoot than adult birds. This is supposed by the fact that the juvenile:adult ratio in the autumn bag 1970 and 1971 was 2.64:1 and 2.72:1 (see p. 24) as opposed to 1.5:1 in woodcock ringed in autumn. The way, in which the birds have been caught, gives no reason to suggest that juveniles are easier to catch than adults.

If a woodcock population is to be maintained at a fixed level, then the number of adults which die during a year must

Country of ringing	Period	No. of recoveries used	Mean annual mortality in adults %	First-year mortality %	Source
Denmark, Norway, Sweden, Finland	1899–1967	227	50.6 ± 4.0	65.6	This study
Holland	1911–1967	39	50.0 ± 5.6		This study
Scotland and N England	1891–1930	203	abt. 37	56	LACK (1943)
Britain and Ireland	1891–1954	251	40.7 ± 2.26	55	BOYD (1962)
Britain and Ireland	1921–1930		34.3 ± 3.48		BOYD (1962)
Britain and Ireland	1931–1940		46.5 ± 3.31		BOYD (1962)
Baltic states	up to 1953	29	43.9 ± 6.11		BOYD (1962)

Table 27. The mean annual mortality rate for woodcock. The calculated mortality from Holland is based on recoveries of ringed migrants which originated chiefly from Scandinavia.

be balanced by the number of juveniles which survive until the next breeding season. It is supposed that woodcock are mature in their first breeding season. This assumption is supported by studies on woodcock from the spring season (1 March–7 April), which showed that in young males (hatched the previous year) the testes contained fertile sperm. In young females the development of the ovary was about the same stage as in adult females. KRAFFT (1972) mentions a control of a ringed pullus 13 months later incubating 4 eggs. Calculations of mortality rate indicate that of 100 adult woodcock, 51 die before the next season. These must therefore be replaced by a similar number of juveniles. Since the first-year mortality rate is 65.6 %, this means that 100 adults (50 males and 50 females) must produce 147 fully-fledged juveniles if 51 are to survive until the following breeding season. This corresponds to a ratio of 1.47 juveniles per adult (or more accurately, 2.94 juveniles per adult female). This former value is in excellent agreement with the juvenile: adult ratio found in woodcock captured for ringing in autumn, 103 of which were determined as to age, and in which the juvenile:adult ratio was calculated to be 1.5:1. At the beginning of the breeding season, a sample of 100 individuals should therefore be composed of 49 adults and 51 juveniles, with a juvenile: adult ratio of 1.04:1.

The woodcock is a determinate layer of 4 eggs, 3.84 eggs being the average for 330 clutches (ALEXANDER 1946). Out of 86 nests discovered and of which the subsequent fate was known, 34 (40 %) were abandoned or suffered predation (CLAUSAGER 1973b). In such cases, a new clutch is normally produced. The hatching success for clutches which are incubated to completion is high; BOYD (1962) gives a value of 89 %. Using the data of ALEXANDER (1946), MCCABE & BRACKBILL (1973) calculated the mortality rate in the first month after hatching to be 22 %. No information was given on the way in which this figure was reached, but mortality at this stage is undoubtedly high. Another factor to be considered is the amount of mortality occurring in breeding adults during the breeding season, and likewise it is probable that a few birds do not breed, or are incapable of breeding due to such factors as disease or previous shooting wounds.

When the number of eggs produced (3.84 per nest) is reduced by the percentage which do not hatch (11 %) and the mortality rate during the first month of life (22 %), a value of 2.66 fully-fledged young per adult female is obtained. This is a maximum value, which is further reduced by the factors mentioned just previously. Comparing this value with the number of fully-fledged young which must survive in order to balance mortality in the adult population (2.94 per adult female), it is obvious that even the maximum figure of 2.66 juveniles/adult female is too low, and that, if it is correct a considerable proportion of the population must lay two clutches to maintain population stability.

Summary

During 1968–1972, the Game Biology Station carried out a study of the occurrence and shooting utilization of woodcock in Denmark.

The present paper describes the migration of woodcock breeding in Scandinavia, on the basis of recoveries of individuals ringed in Denmark, Norway, Sweden and Finland. In addition, woodcock migration through Denmark is analysed in various ways, including the effect of weather conditions on the migration itself, and the mean annual mortality rate and population turnover rate are calculated.

2,538 woodcock have been ringed in the four Scandinavian countries up until 31 December 1971 (31 December 1972 for Denmark), and 327 were recovered by 31 December 1972 (31 December 1973 for Denmark) (Tables 1 & 2); 91 % of these were recovered as shot (Table 3).

The majority of woodcock in Scandinavia migrate in a south-westerly direction to their winter quarters in western Europe, including the British Isles, France and Spain (Fig. 1). No birds from Norway, 5 % from Sweden, and about 25 % from Finland migrate in a southerly direction to spend the winter in S and SE Europe (Italy, the Balkan peninsula, and Turkey). It is exceptional for woodcock from Scandinavia to travel as far as N Africa. When woodcock migrate, it is generally across a broad front.

The longest migration recorded for woodcock is that of birds from Finland, an average of 2,300 km, while birds from Sweden were shown to travel 1,565 km. and from Norway 1,350 km (Table 10). The mean RR-direction of woodcock ringed as pulli in Finland is 218° as opposed to 224° of those ringed in Sweden and Norway, and 234° of birds ringed as migrants in Denmark. The more westerly tendency for those ringed in Denmark probably is due to some segregation of different populations regarding to winter quarters already when the woodcock arrive in Denmark, so the birds, which pass this country to a higher degree continue to the British Isles to winter there.

In Finland, woodcock begin their autumn migration earlier than in Sweden and Norway (Fig. 2). The real autumn migration starts about mid-October, and by about 20 November almost the whole Scandinavian population has arrived in their winter quarters. Depending on the arrival of spring weather, the birds begin to move back to their breeding grounds in the first half of March. In Denmark they may arrive in early March, while further N and E they arrive later on; in Finland the last of the woodcock do not arrive at their breeding grounds until about mid-May.

Several recoveries indicate that woodcock may also move in winter (Table 13). The majority of birds return to the place in which they were hatched (Table 14), but several recoveries indicate that abmigration occurs, probably because mating in some cases may take place in winter quarters or during the spring migration (Fig. 5). Recoveries of ringed migrants show that woodcock may rest for several days before continuing their migration (Table 15).

Analyses of the sequence of woodcock migration through Denmark show that the main migration in spring occurs during the period 25 March–20 April, and in autumn during 20 October–20 November (Figs. 7 & 8). Migration in each single year was studied using information on bagged woodcock for that year (Figs. 9 & 10).

The influence of weather conditions on the actual migration is shown by the effects of a drop in temperature, clearing sky and decreasing wind speed, which induce the migratory impulse in autumn, and by rising temperature, overcast sky, and wind between S and W, which induce migration in spring (Tables 17 & 18). Of these factors, temperature appears to be the most important, and in spring changes in temperature do not require to be as marked as in autumn to induce the migratory impulse.

In bagged woodcock, the juvenile:adult ratio in autumn was 2.5:1 in 1970 and 2.7:1 in 1971 (Table 20). The distribution of adults and juveniles suggests that the migration of juveniles in autumn is more prolonged than that of adults (Fig. 12). Apparently the woodcock which winter in Denmark are mainly juveniles. In spring 1971 the juvenile:adult ratio was 1.0:1 as opposed to 0.8:1 in 1972 (Table 22). The much lower ratio of juveniles:adults in spring kills compared with that in autumn is considered to be due amongst other things to the fact that the spring juvenile migration occurs later than that of adults, and also that juveniles in autumn are more easily shot than adults.

The sampled population was comprised of equal proportions of males and females. In autumn, no difference in time was discovered between the migration of adult males and females, but in juveniles there was a slight tendency for females to arrive a little earlier than males (Table 23). In spring adult males were the earliest to arrive, followed by juvenile males, adult females and finally juvenile females (Table 25 and Fig. 13).

The mortality rate during the first year of life for woodcock in Scandinavia was calculated to be 65.6 %, and the mean annual mortality rate for adults to be 50.6 ± 4.0 %. For migrants in Holland, which originate in the main from Scandinavia, the mean annual mortality rate was calculated as 50.0 ± 5.6 % for adult birds. The mortality rate for woodcock ringed on migration on Heligoland was of a similar value.

The data given here suggest that if the population of Scandinavian woodcock is to be maintained in numbers, each adult female yearly must produce an average of 2.94 fully-fledged young. This would appear to be possible only if a considerable proportion of the population lay two clutches of eggs annually, as some nests and young are destroyed during incubation and development.

Dansk resumé

Skandinaviske skovsneppers *(Scolopax rusticola)* træk.

I årene 1968–1972 foretog Vildtbiologisk Station undersøgelser af skovsneppens forekomst og jagtlige udnyttelse i Danmark.

Nærværende artikel behandler trækforholdene for de i Skandinavien yngle-lende skovsnepper på grundlag af genmeldinger af individer, mærket i Danmark, Norge, Sverige og Finland. Endvidere er skovsneppens træk gennem Danmark analyseret på forskellig måde (herunder også vejrforholdenes indflydelse på selve trækket), ligesom der er

foretaget beregninger af gennemsnitlig årlig dødelighed og bestandsomsætning.

Der er indtil 31. december 1971 (Danmark 31. december 1972) ringmærket 2.538 skovsnepper i de 4 skandinaviske lande, hvoraf 327 er blevet genmeldt pr. 31. december 1972 (Danmark 31. december 1973) (Tabel 1 og 2). 91 % er genmeldt som skudt (Tabel 3).

Hovedparten af de skandinaviske skovsnepper trækker i sydvestlig retning til overvintringskvarterer i det vestlige Europa (de Britiske Øer, Frankrig og Iberiske Halvø (Fig. 1). Ingen af de norske, ca. 5 % af de svenske og ca. 25 % af de finske fugle trækker i sydlig retning for at tilbringe vinteren i det sydlige og sydøstlige Europa (Italien, Balkan og Tyrkiet). Kun undtagelsesvis når de skandinaviske skovsnepper til Nordafrika. Skovsneppen foretager overvejende et bredfronttræk.

De finske skovsnepper foretager det længste træk (i gennemsnit 2.300 km), de svenske 1.565 km og de norske 1.350 km (Tabel 10). Den gennemsnitlige RR-retning (retning mellem mærknings- og genmeldingssted) for skovsnepper mærket i Finland er 218° mod 224° for fugle mærket i Sverige og Norge og 234° for skovsnepper mærket i Danmark. Den mere vestlige tendens blandt de fugle, som er mærket i Danmark i træktiden, skyldes sandsynligvis, at der allerede, når fuglene ankommer til Danmark, er sket en vis udspaltning hos de forskellige populationer med hensyn til vinterkvarterer, således at de skovsnepper, som passerer Danmark, i højere grad fortsætter til de Britiske Øer for at tilbringe vinteren der.

De finske skovsnepper indleder efterårstrækket tidligere end de svenske og norske (Fig. 2). Det egentlige efterårstræk begynder omkring midten af oktober, og omkring 20. november har næsten hele den skandinaviske bestand nået vinterkvartererne. I første halvdel af marts (afhængig af forårets komme) begynder fuglene at begive sig af sted mod ynglepladserne. Ankomsten til disse kan for de danske fugles vedkommende ske allerede i første halvdel af marts. Længere nord- og østpå ankommer fuglene senere, og i Finland er de sidste skovsnepper først på ynglepladserne omkring midten af maj.

Flere genmeldinger viser, at skovsneppen kan foretage vintertræk (Tabel 13). Hovedparten af skovsnepperne vender tilbage til de steder, hvor de er udklækket, men flere genmeldinger viser, at abmigration forekommer, sandsynligvis fordi der kan ske en udparring i vinterkvarteret eller under forårstrækket (Fig. 5). Genmeldinger af mærkede trækgæster viser, at fuglene kan raste adskillige dage, før trækket fortsættes (Tabel 15).

Analyser af skovsneppens træk tidsmæssigt set gennem Danmark viser, at hovedtrækket om foråret foregår i perioden 25. marts–20. april og om efteråret fra 20. oktober–20. november (Fig. 7 og 8).

Trækket det enkelte år er belyst på grundlag af oplysninger om nedlagte skovsnepper de enkelte år (Fig. 9–10).

Vejrforholdenes indflydelse på selve trækket viser, at temperaturfald, opklaring og aftagende vind udløser trækdriften om efteråret, mens temperaturstigninger, overskyet himmel og vind mellem S og W udløser trækdriften om foråret (Tabel 17 og 18). Temperaturen synes at være den mest betydningsfulde faktor. Temperaturændringerne skal ikke

være så store om foråret som om efteråret for at udløse trækdriften.

Juvenil/adult forholdet blandt nedlagte skovsnepper var i efteråret 1970 2,5 og 2,7 i 1971 (Tabel 20). Fordelingen af adulte og juvenile fugle viser, at de juveniles træk om efteråret er mere udstrakt end de adultes (Fig. 12). Tilsyneladende er de i Danmark overvintrende skovsnepper overvejende juvenile individer. I foråret 1971 var juv./ad. forholdet 1,0 mod 0,8 i 1972 (Tabel 22). Det meget lavere juv./ad. forhold om foråret i forhold til efteråret skyldes blandt andet, at de juveniles forårstræk falder senere end de adultes, men også at juvenile skovsnepper om efteråret nedlægges lettere end adulte.

Bestanden rummer lige mange hanner og hunner. Om efteråret er der ikke konstateret nogen tidsmæssig forskel i de adulte hanner og hunners træk, mens der for de juvenile er en tendens til, at hunnerne begynder trækket lidt tidligere end hannerne (Tabel 23). Om foråret trækker adulte hanner tidligst, så de juvenile hanner, adulte hunner og til sidst de juvenile hunner (Tabel 25 og Fig. 13).

Førsteårsdødeligheden blandt de skandinaviske skovsnepper er beregnet til 65,6 %, og den gennemsnitlige årlige dødelighed for adulte til 50,6 % ± 4,0 %. Dødeligheden blandt hollandske trækgæster (der i stor udstrækning kommer fra Skandinavien) er 50,0 % ± 5,6 % for adulte. Dødeligheden for skovsnepper, mærket i træktiden på Helgoland, er af tilsvarende størrelse.

Såfremt der skal være balance i den skandinaviske bestand, skal hver hun i gennemsnit årligt producere 2,94 flyvedygtig unge. Dette kan ikke lade sig gøre, med mindre en betragtelig del af bestanden lægger to kuld årligt, fordi en del reder og unger går til under udrugningen og opvæksten.

Резюме на русском языке

МИГРАЦИЯ СКАНДИНАВСКОГО ВАЛЬДШНЕПА

(*Scolopax rusticola*)

С 1968 по 1972 г. Станция Исследования Биологии Дичи провела исследование распространения и охотничей добычи вальдшнепа в Дании.

В настоящей статье обсуждается миграция гнездящихся в Скандинавии вальдшнепов на основании сообщений о птицах, помеченных кольцами в Дании, Норвегии, Швеции и Финляндии. Кроме того, миграция вальдшнепов через Данию анализируется разными способами, принимая в учет влияние метеорологических условий на самую миграцию, а также произведены вычисления средней годовой смертности и оборота популяции.

До 31 декабря 1971 г. (в Дании до 31 декабря 1972 г.) в четырех скандинавских странах были помечены кольцами 2538 вальдшненов, а до 31 декабря 1972 г. (в Дании до 31 декабря 1973 г.) были получены сведения о 327 (табл. 1 и 2). 91 % этих птиц были убиты охотниками.

Наибольшая часть вальдшнепов Скандинавии мигрирует в югозападном направлении в местности их зимовки в Западной Европе, включающие Британские Острова, Францию и Испанию (Фиг. 1). Никакие из птиц Норвегии, 5 % птиц из Швеции и около 25 % птиц из Финляндии мигрируют в южном направлении чтобы проводить зиму в Южной и Юговосточной Европе (в Италии, на Балканском Полуострове и в Турции). Только в исключительных случаях вальдшнепы из Скандинавии перелетают до самой

Северной Африки. Перелеты вальдшнепов обычно происходят широким фронтом.

Самый дальный перелет предпринимают вальдшнепы из Финляндии, в среднем 2300 км, между тем как птицы из Швеции совершали перелеты в 1565 км, а из Норвегии 1350 км (Табл. 10). Среднее направление перелета с места кольцевания к местам, откуда получены сообщения о вальдшнепах помеченных в Финляндии, будучи еще птенцами, составляет 218°, для птиц, помеченных в Швеции и Норвегии – 224°, а для птиц, помеченных в Дании во время перелета – 234°. Более западная тенденция особей, помеченных в Дании, вероятно объясняется тем, что разные популяции уже при их прибытии в Данию до некоторой степени разделены по местностям зимовки, так что перелетающие эту страну птицы в более высокой степени продолжают свой перелет на зимовку на Британских Островах.

В Финляндии вальдшнепы начинают свой осенний перелет немного раньше, чем в Швеции и Норвегии (Фиг. 2). Настоящая осенняя миграция начинается около середины сентября, и до прибл. 20 ноября почти вся скандинавская популяция прибывает на места зимовки. При наступлении весенней погоды, птицы начинают перелетать обратно на гнездовья в первой половине марта. В Данию они могут прибывать уже в начале марта, между тем как далее к северу и востоку они прибывают позднее, а в Финляндию последние вальдшнепы не прибывают на гнездовья до прибл. середины мая.

Несколько сообщений о встречах птиц указывают на то, что вальдшнепы могут перелетать и зимой (Табл. 13). Большинство птиц возвращается в те же места, где они были выведены (Табл. 14), но несколько сообщений свидетельствуют о том, что происходит также и уход, вероятно потому, что птицы в некоторых случаях спариваются на месте зимовки или во время весенней миграции (Фиг. 5). Сообщения о помеченных кольцами птицах показывают, что вальдшнепы иногда останавливаются на одном месте на несколько дней перед тем, как продолжать перелет (Табл. 15).

Анализы последовательности перелетов вальдшнепов через Данию показывают, что главная миграция весной происходит в течение периода с 25 марта по 20 апреля, а осенью с 20 октября по 20 ноября (Фиг. 7 и 8). Перелеты каждого отдельного года были исследованы на основании сведений о вальдшнепах, убитых охотниками в соответствующем году (Фиг. 9 и 10).

Влияние метеорологических условий на самые перелеты выражается тем, что понижения температуры, прояснение и понижение скорости ветра вызывают побуждение к перелету осенью, а повышения температуры, пасмурная погода и ветры с юга или запада вызывают миграцию весной (Табл. 17 и 18). Важнейшим из этиих условий кажется температура. Весной для возбуждения склонности к перелету не требуется таких сильных изменений температуры, как осенью.

В составе охотничей добычи вальдшнепов, количественное соотношение молодых и взрослых птиц осенью составляло 2,5:1 в 1970 г. и 2,7:1 в 1971 г. (Табл. 20). Распределение взрослых и молодых птиц указывает на то, что миграция молодых особей осенью продолжается дольше миграции взрослых (Фиг. 21). Кажется, что зимующие в Дании вальдшнепы главным образом молодые. Весной 1971 г. соотношение молодых и взрослых составляло 1,0:1, а в 1972 г. – 0,8:1 (Табл. 22). Можно предполагать, что гораздо более низкое соотношение молодых и взрослых в весенней охотничей добыче отчасти объясняется тем, что весенний перелет молодых птиц происходит позднее перелета взрослых, а отчасти тем, что осенью бывает легче убивать молодых птиц, чем взрослых.

Образец популяции составляется из одинакового числа самцов и самок. Осенью не было обнаружено разницы времени миграции взрослых самцов и самок, но у молодых была некоторая тенденция к более раннему прибытию самок, чем самцов (Табл. 23). Весной взрослые самцы прибывали первыми, затем прибывали молодые самцы, взрослые самки, а последними – молодые самки (Табл. 25 и Фиг. 13).

Вычисленная смертность вальдшнепов Скандинавии в первом году их жизни составляла 65,6%, а средняя годовая смертность взрослых особей была равна $50,6 \pm 4,0$%. Для

вальдшнепов, перелетающих через Голландию, которые главным образом являются птицами скандинавского происхождения, вычислена средняя годовая смертность взрослых особей в 50,0 ± 5,6 %. Приблизительно такая-же смертность вычислена для вальдшнепов, помеченных кольцами на острове Гельголанде во время перелета.

Указанные в этой статье данные дают основание предполагать, что для поддержания численности популяции скандинавского вальдшнепа каждая самка ежегодно должна выводить средним числом 2,94 вполне оперившихся птенцов. Кажется, что это возможно только при условии, что значительная часть популяции способна выводить птенцов два раза в год, так как часть гнезд и птенцов погибают во время высиживания и развития.

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