DANISH REVIEW OF GAME BIOLOGY Vol. 12 no. 1

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by

BJARNE BAK & HENNING ETTRUP

Med et dansk resumé:
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trækforhold og dødelighed

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Условия миграции и смертность датских чибисов
(Vanellus vanellus)

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Abstract

Analyses of the geographical and temporal migration pattern in the Danish Lapwing *(Vanellus vanellus)* based on 1,085 recoveries of birds ringed as chicks are carried out by computer assistance. Movements during the summer period as well as homing and abmigration are studied. Mortality, population turnover and requisite production for maintenance of the population are calculated and compared with the production in different breeding habitats.

Introduction

In connection with studies on the breeding biology of the Lapwing *(Vanellus vanellus)* carried out during 1977-79, analyses of the migration pattern of the Danish population were performed. Earlier the migration of the Lapwing has been treated in a traditional way by SKOVGAARD (1928), SALOMONSEN (1938 & 1972) and ROSENDAHL & SKOVGAARD (1970). IMBODEN (1974), by means of computer techniques, analysed the migration of the different European Lapwing populations. Larger analyses of this type have been facilitated by the EURING cooperation (PERDECK & SPEEK 1966), with standardisation of ringing and recovery data.

The present paper has very much been inspired by the work of IMBODEN, as several of his methods have been used directly or in another form, and the applicability of the methods has also been evaluated. In addition to analysing the geographical and temporal sequence of the migration, homing, movements in summer and abmigration are also described. In considering the last phenomena, recoveries of Lapwings ringed abroad and found in Denmark have also been included. Finally, calculations have been performed of mortality and turnover in the Danish Lapwing population.

The authors would like to thank A. H. JOENSEN and I. CLAUSAGER for valuable advice, T. LAURSEN for assistance with solving initial problems in programming and use of the computer, and A. EJLERSEN for advice concerning the statistical computations. Thanks are also due to N. O. PREUSS for providing access to ringing and recovery data of the Zoological Museum, Copenhagen, on Lapwings, and to C. IMBODEN for making available his recovery data.

Material and methods

Recoveries of 1,244 Lapwings ringed in Denmark have been collected. Of these, 130 were ringed as full growns and as their place of origin was thus unknown they were omitted from further calculations. Another 29 recoveries were similarly omitted due to incomplete information (missing date of recovery, place, etc.). The data used thus comprised 1,085 recoveries of Lapwings ringed as chicks in Denmark during 1920-1978 (Table 1).

The recovery rate can only be given approximately, as the total ringing data was not available. However, of 14,944 Lapwings ringed as chicks 708 were later recovered, corresponding to 4.7%.

Of the 1,085 recoveries, 80 were controls (Table 1), of which 79 were from Denmark (47 as chicks and 32 later as juveniles or adults). These are dealt with separately in the section concerning homing (p. 14).

In further treatment of the data, the recoveries are divided into two groups. The first of these is comprised of birds recovered prior to August 1st in the year after ringing (Table 2), and birds in this group will hereafter be referred to as juveniles, even although this group may include birds which according to the usual definition are no longer juveniles. The second group consists of birds recovered after July 31st in the year following ringing (Table 3), these birds being referred to as adults. This division was made in order to analyse the residence of juvenile birds in their first breeding season.

In addition to the above data, 246 recoveries of Lapwings ringed as chicks abroad and recovered in Denmark were collected. These were used in connection with a study on immigration (pp. 15-16).

By dealing with a large number of recovery data by computer assistance, it becomes possible in a short time to produce

Reported recovery cause / Country of recovery	Shot/killed	Controlled	Found dead	Weather	Wires	Traffic	Predated	Other causes	Unknown	Total
U.S.S.R.	2	–	1	–	–	–	–	–	–	3
Finland	–	–	2	–	–	–	–	1	–	3
Sweden	–	–	6	–	1	–	1	–	–	8
Norway	–	–	2	–	–	–	–	–	–	2
Denmark	265	79	182	6	15	14	11	1	–	573
W. Germany	1	–	9	–	–	–	1	2	1	14
Holland	1	–	7	1	–	–	–	–	1	10
Belgium	1	–	1	–	–	–	–	–	4	6
British Isles	38	–	19	–	1	–	–	3	16	77
France	166	1	25	–	–	–	1	–	31	224
Spain	78	–	8	–	–	–	–	–	34	120
Portugal	16	–	3	–	–	–	–	–	5	24
Italy	1	–	1	–	–	–	–	–	–	2
Poland	–	–	1	–	–	–	–	–	–	1
Morocco	11	–	2	–	–	–	–	–	3	16
Algeria	–	–	–	–	–	–	–	–	1	1
Azores	1	–	–	–	–	–	–	–	–	1
Total	581	80	269	7	17	14	14	7	96	1085

Table 1. Recoveries of 1,085 Lapwings during the period 1920-1978, arranged according to country and cause of recovery. All birds were ringed as chicks in Denmark.

Country of recovery	Month of recovery Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
Finland	1	–	–	–	–	–	–	–	–	–	–	–	1
Sweden	–	1	–	–	–	–	–	–	–	–	–	–	1
Norway	–	–	–	–	–	–	–	–	–	–	–	1	1
Denmark	14	17	44	40*	107	45	34	8	1	1	1	3	315
W. Germany	–	–	–	1	1	–	1	–	2	–	–	2	7
Holland	1	1	–	–	–	–	1	2	–	1	–	–	6
Belgium	–	–	–	–	–	–	–	–	1	1	–	1	3
British Isles	–	–	–	–	1	1	5	4	6	3	8	–	28
France	1	–	–	–	–	–	1	4	24	22	15	16	83
Spain	–	–	–	–	–	–	–	2	12	26	18	3	61
Portugal	–	–	–	–	–	–	–	–	5	3	2	2	12
Italy	–	1	–	–	–	–	–	–	–	–	–	–	1
Morocco	–	–	–	–	–	–	–	1	1	3	1	–	6
Azores	–	–	–	–	–	–	–	–	1	–	–	–	1
Total	17	20	44	41	109	46	42	21	53	60	45	28	526

Table 2. Recoveries of 526 Lapwings ringed as chicks in Denmark and recovered before August 1st of the subsequent year. Controls were omitted from results.

* Includes one recovery from a fishing-boat in the North Sea.

maps showing the migratory movements contrary to the traditional method which is very timeconsuming. The method describes the distribution of the total population in a given period, using calculated mean coordinates and standard deviations.

IMBODEN (1974), who used this method, calculated the standard deviation in a N-S and E-W directions. As the migration is more directed NE-SW (and opposite), the calculated standard deviations N-S and E-W give a false picture of the real distribution of the Lapwing population over a certain period. This is illustrated in Fig. 1, where the mean coordinates and the standard deviations N-S and E-W for adult Lapwings recovered during March are compared with the more NE-SW, NW-SE directed standard deviations. The latter are based on the calculated direction of migration in the same month. The calculated standard deviations N-S and E-W give the impression that the population is equally distributed in all directions, whereas the corresponding ones calculated in NE-SW and NW-SE directions show the more realistic distribution of the population along the migration route, and at right angles to it, in a certain period.

As the migratory movements of birds occur over the surface of a globe, it is necessary to allow for the curvature of the earth in calculating mean coordinates. For this purpose the loxodromic formula of IMBODEN & IMBODEN (1972) was used. The direction of dispersal in a given period is calculated using a linear regression based on the actual recovery site coordinates expressed in a coordinate system, with zero latitude (the equator) as the x-axis and zero longitude (Greenwich) as the y-axis. From these, the equation $y = a + bx$ for the line of best fit is calculated. From the values found for a and b, the angle (v) formed by this line and the x-axis is calculated, together with the point of intersection (P) of this line with the x-axis. As standard deviations in the direction of dispersal and at right angles to it are required, all coordinates are transformed to a new coordinate system with its origin

Country of recovery	Month of recovery Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
U.S.S.R.	1	1	-	-	-	1	-	-	-	-	-	-	3
Poland	-	-	-	-	1	-	-	-	-	-	-	-	1
Finland	2	-	-	-	-	-	-	-	-	-	-	-	2
Sweden	1	4	1	-	-	-	-	-	-	-	-	1	7
Norway	-	-	-	-	-	-	-	-	-	-	-	1	1
Denmark	23	19	8	3	45	33	29	8	1	-	-	10	179
W. Germany	3	-	-	1	-	-	-	1	2	-	-	-	7
Holland	1	-	-	-	-	-	-	2	-	-	-	1	4
Belgium	-	-	-	-	-	-	-	-	2	-	1	-	3
British Isles	-	1	1	-	-	1	4	10	3	20	7	2	49
France	1	-	-	-	-	-	2	5	41	41	21	29	140
Spain	1	-	-	1	-	-	-	2	6	26	20	3	59
Portugal	-	-	-	-	-	-	-	-	-	8	4	-	12
Italy	-	-	-	-	-	-	-	-	-	1	-	-	1
Morocco	2	-	-	-	-	-	-	-	4	3	1	-	10
Algeria	-	-	-	-	-	-	-	-	-	1	-	-	1
Total	35	25	10	5	46	35	35	28	59	100	54	47	479

Table 3. Recoveries of 479 Lapwings ringed as chicks in Denmark and recovered after July 31st in the year after ringing. Controls were omitted from results.

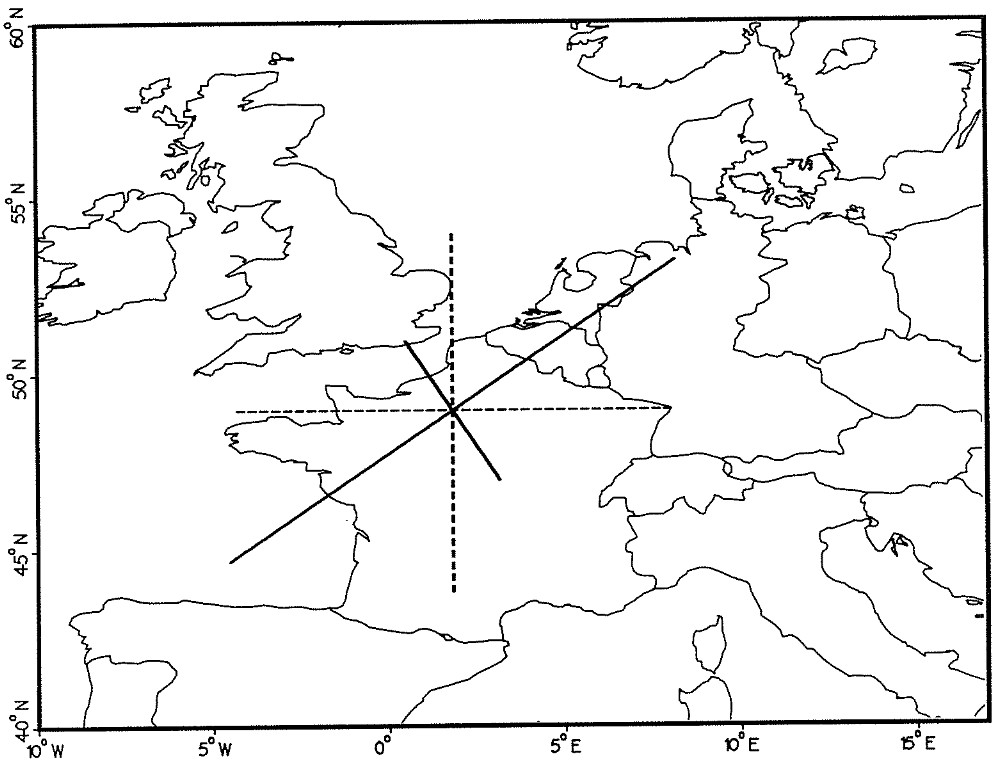


Fig. 1. Mean coordinates and standard deviations of adult Lapwings recovered during March.
Dotted lines: standard deviations N-S and E-W.
Solid lines: standard deviations in the direction of migration, and at right angles to it.

at P, and rotated such that the x-axis of the new system is coincident with the regression line (see example, Fig. 2). The mean coordinate and associated standard deviations are calculated for this new system, and drawn on a map of equidistant Mercator projection (Fig. 6).

Although the mean coordinate does not itself indicate anything specific about where individual Lapwings are recovered, it, and in particular the standard deviations, does give an impression of the dispersal of the whole population.

For the treatment of the data, a CDC Cyber datamat was used at RECAU (the Regional Computing Centre at Aarhus University). The programmes used were mainly written in FORTRAN, but a few were in PASCAL. Separation was carried out using the SPSS facility (Statistical Package of Social Science), and some of the statistical routines used were obtained from the public library NAGLIB, (Numerical Algorithm Group Library). Figures were produced using the graphic system DISSPLA and the Hewlett-Packard plotter at RECAU.

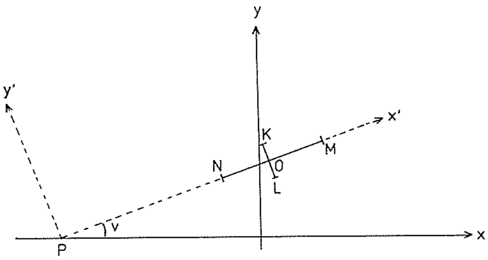


Fig. 2. Transformation of the original coordinate system (x, y) into a new one (x', y').
The lines K-L and M-N indicate standard deviations.

Geographical and temporal sequence of migration

The monthly distribution of recoveries according to country of recovery for the two age-groups is given in Tables 2 & 3. The exact recovery sites for the months of October-April are shown in Figs. 3 & 4. Fig. 5 shows for each recovery the distance between ringing-and recovery place (RR-distance), calculated according to formulae in KERN (1962) and IMBODEN & IMBODEN (1972). The mean coordinates, standard deviations and mean RR-distance calculated for each month from October to April are given in Table 4.

The autumn migration generally begins in October (Fig. 5). The first foreign recovery of a juvenile Lapwing is from Great Britain, on October 13th. An adult bird was however already recovered on the 10th, but may have abmigrated (see p. 14). However, for a bird as dependent on the weather as the Lapwing (SALOMONSEN 1938), annual variation in weather conditions can lead to considerable differences in the time of departure; in particular the departure may be delayed and in mild winters Lapwings may even winter in Denmark. In both age groups, there is a tendency for the preferred direction of migration to be directly west to Britain, while the SW migration along the continental coast is less used (Tables 2 & 3, Figs. 3 & 4). It should however be emphasized that differences in shooting intensity in individual countries can lead to a systematic error in such comparisons (IMBODEN 1974). As the Lapwing is not a game bird in West Germany and Holland, it is likely that these countries are under-represented as regards recoveries during the autumn migration, and their importance thus undervalued. It is however noticeable that the number of recoveries from Belgium, which has an open season for Lapwings (LAMPIO 1974), is also very low (6 recoveries in the period December-March).

In November there is still a positive bias in the number of recoveries from the British Isles, but recoveries from France are increasing (4 juveniles and 5 adults), and in both age-groups two recoveries from northern Spain exist. One juvenile even reached Morocco (2,700 km) on November 2nd.

Lapwings reach their actual winter quarters during December. The most important areas are France, the Iberian peninsula, Morocco, and the British Isles. As already mentioned, some may even winter as far north as Denmark, especially in mild winters. For instance, one 5½ year old bird was recovered on December 19th at the ringing site at Ringkøbing fiord, and three juveniles, all ringed in Sealand, were recovered on December 28th (55 km from ringing site), January 12th (at ringing site), and February 13th (13 km from ringing site), respectively. The last of these may possibly have been an early-returning bird.

There appears to be a tendency towards a difference in the RR-distance for the two age-groups during the course of winter, as on average, juveniles have an RR-distance which is 100-150 km greater than that of the adults (Fig. 5 & Table 4).

ROSENDAHL & SKOVGÅRD (1970) have earlier discussed the extent to which some Lapwings may winter in the British Isles, or whether the entire population winters on the Continent. Taking January and February together, 17.5% of the adult birds and 10.5% of juveniles are recovered from the British Isles. Furthermore, if causes of recovery are considered (Table 1), it is evident that while shooting accounts for 49.4% of all recoveries from the British Isles, the corresponding figure from France and the Iberian peninsula is 70.7%. This means that the probability of recovery in these last two is greater,

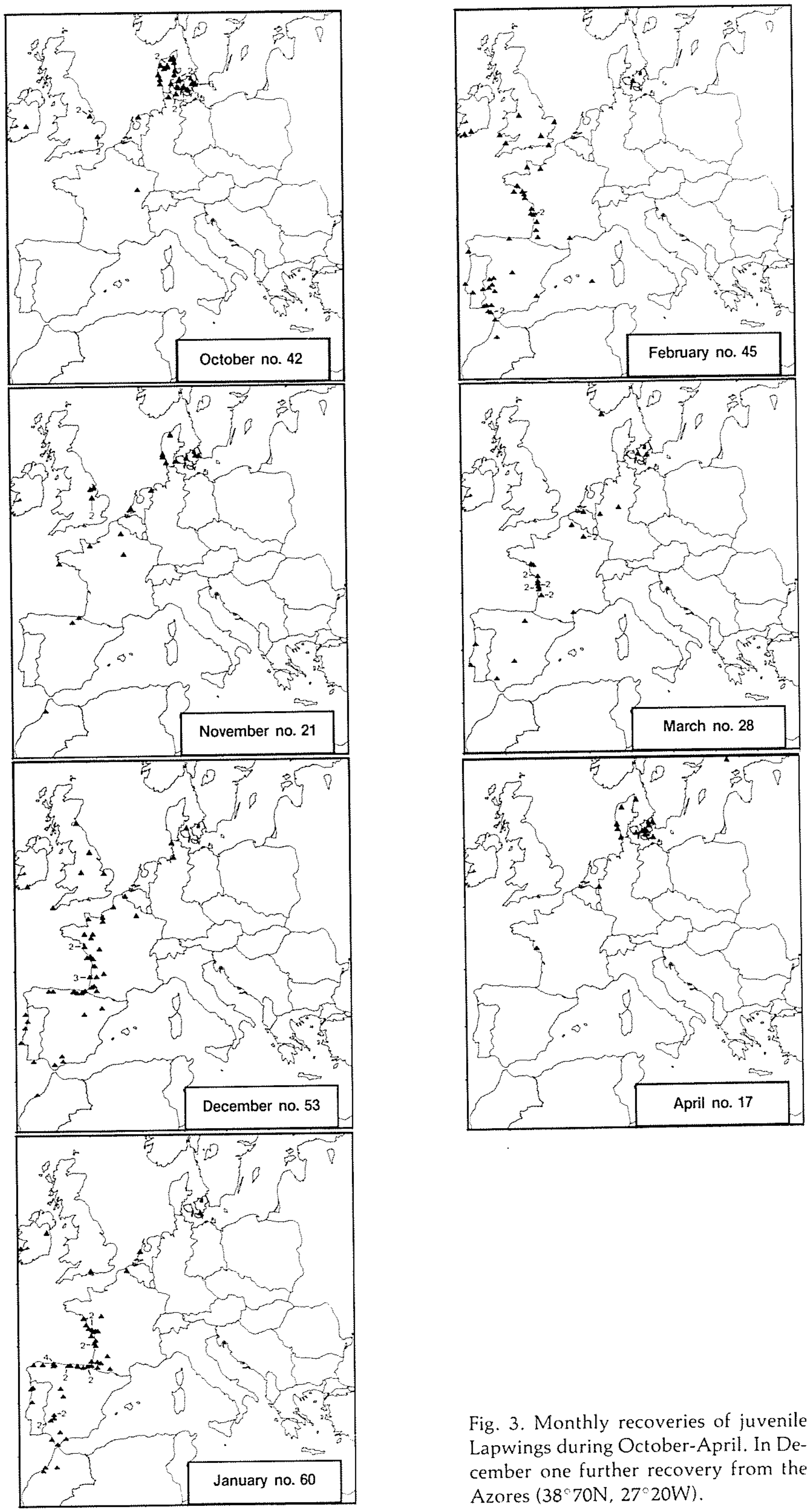


Fig. 3. Monthly recoveries of juvenile Lapwings during October-April. In December one further recovery from the Azores (38°70N, 27°20W).

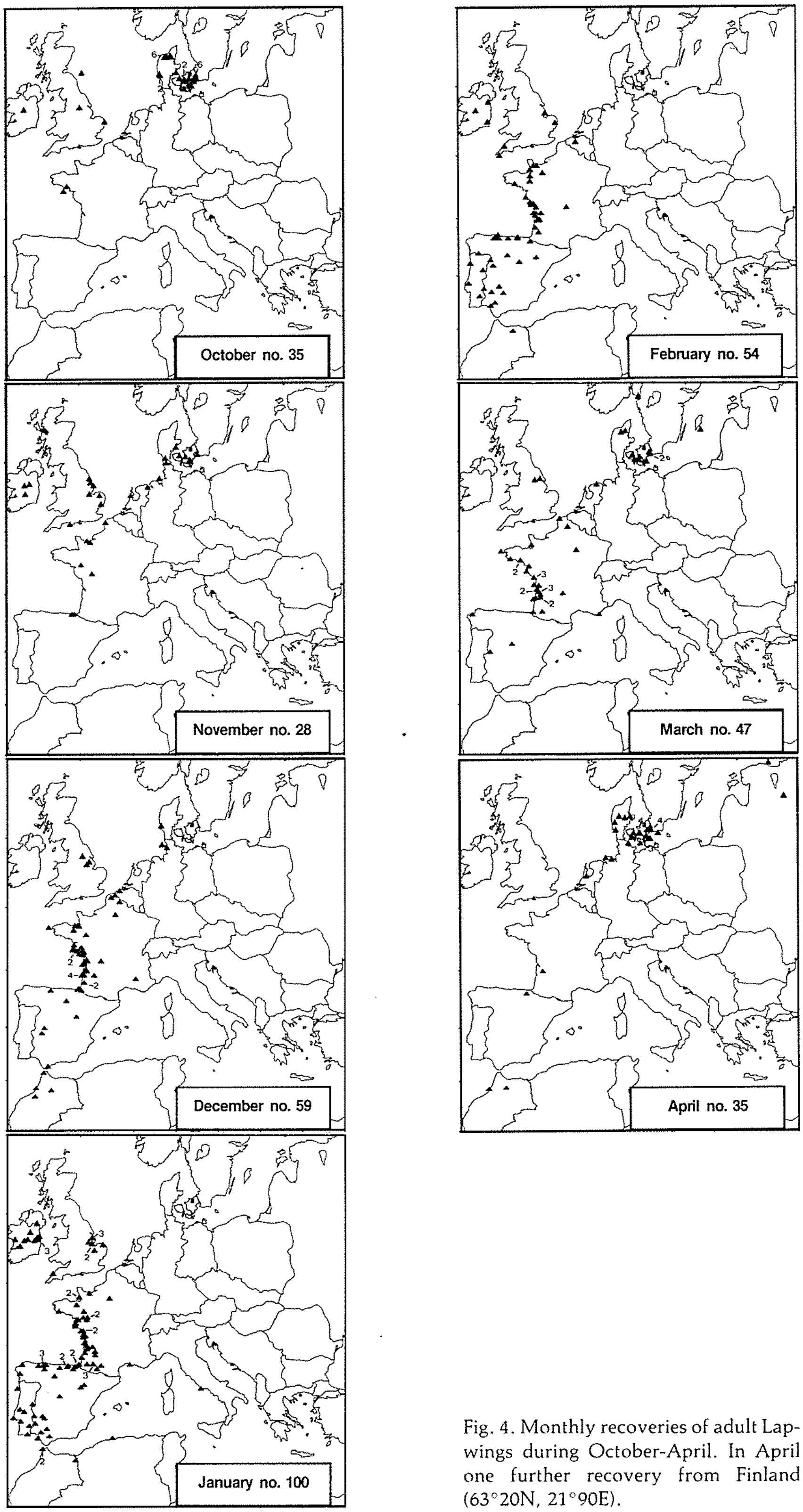


Fig. 4. Monthly recoveries of adult Lapwings during October-April. In April one further recovery from Finland (63°20N, 21°90E).

whereby the importance of the British Isles as winter quarters is underestimated. It is quite obvious that a considerable proportion of the Danish Lapwing population, both juvenile and adult, overwinter in the British Isles.

The spring migration back to Denmark begins in late February-early March. While the autumn migration to winter quarters lasts for about 2½ months, migration to the breeding grounds takes place over about 1½ months (Fig. 5), and is more or less completed by the end of March. The spring migration routes can be studied only very little from recoveries. The low number of recoveries from the British Isles (2 adults in March) and the relatively higher number from Holland, Belgium and West Germany (4 juveniles and 5 adults) in March-April indicate that the Lapwings tend more to follow the continental coastline back to Denmark.

Recoveries from late winter and spring indicate that juveniles may start their return a little later than adults (Fig. 5). However, the differences are so small that more recoveries are needed to verify this point (see also pp. 11-13).

Maps showing the general migration pattern (Fig. 6) are based on the calculated mean coordinates and standard deviations (Table 4). They show that in those months where Lapwings are migrating between breeding areas and winter quarters, the area of dispersal is an elongated ellipse with large standard deviations in the SW-

	Juv.				Ad.			
Period	No. of recoveries	Mean coordinates	Standard deviations*	Mean RR-distance km	No. of recoveries	Mean coordinates	Standard deviations*	Mean RR-distance km
October	42	8°96E 55°20N	4°39 1°32	45	35	8°15E 55°27N	5°42 1°61	190
November	21	3°42E 51°45N	7°31 2°67	710	28	2°50E 52°20N	6°45 2°76	694
December	53	2°48W 45°58N	6°56 3°55	1510	59	1°13W 45°85N	5°34 2°15	1403
January	60	3°38W 43°51N	4°91 3°01	1721	100	3°02W 45°15N	3°79 5°01	1583
February	45	3°39W 43°84N	5°52 4°22	1700	54	3°34W 44°75N	4°18 3°45	1598
March	28	0°72E 47°19N	7°31 1°63	1203	47	1°80E 48°96N	7°64 2°38	1025
April	17	10°08E 55°22N	4°93 1°12	186	35	9°67E 53°89N	8°58 2°43	380

Table 4. Monthly mean coordinates, standard deviations (1/100°), and RR-distance during October-April.

* above: S.D. in direction of migration
below: S.D. at right angles to direction of migration.

NE facing direction of migration and small ones at right angles to it (Table 4). In January-February the Lapwings move only little, and the standard deviations are approximately equally large in both directions, meaning that the dispersal in the winter months is almost circular in shape.

Fig. 6 gives a reasonable indication of the tendency described earlier, towards a westerly-orientated autumn migration very much occurring over the British Isles, while the spring migration occurs more directly in a north-easterly direction. In addition, temporal differences in the dispersal of the birds during the migration are shown by the maps. It is clear that calculations of mean values could be more reliable for those months where only few recoveries are available. A larger number of recoveries in these months (e.g. April and November) would reduce the effect on the mean coordinate of a few greatly deviating recoveries. For instance, two recoveries of adult birds from Morocco in April greatly influenced the mean coordinate and standard deviation for this month. A larger number of recoveries would also enable a more detailed division of time intervals, and thus better illustrate differences in time of the main migration.

In order to examine possible differences in the migration and winter quarters of the juvenile and adult population, non-parametrical tests were used. As recoveries

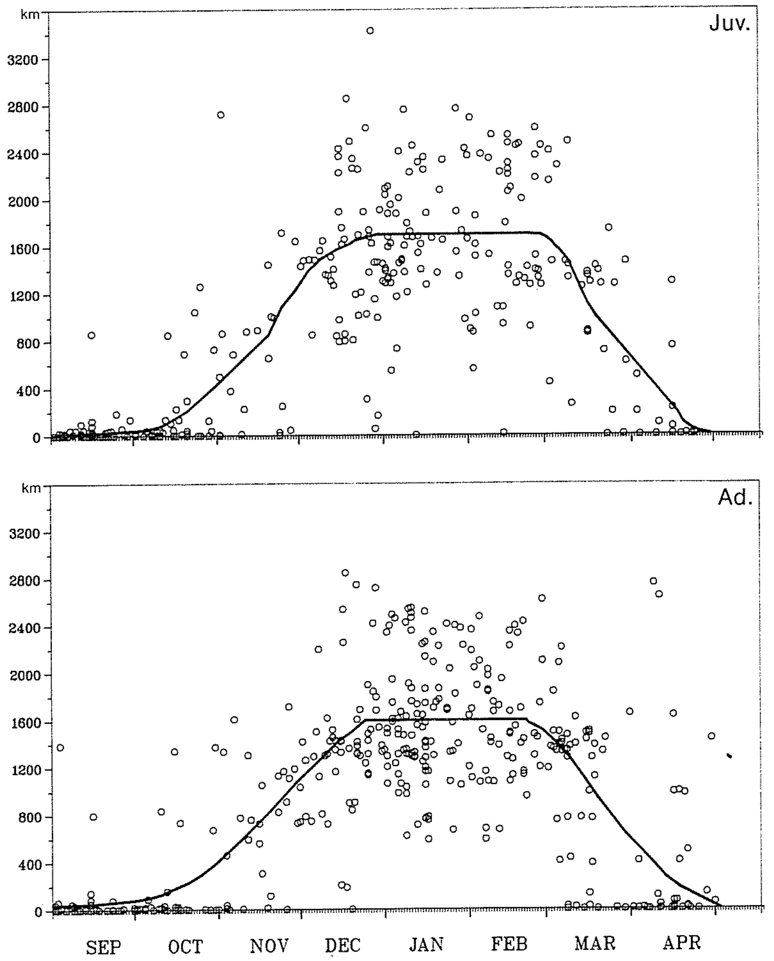
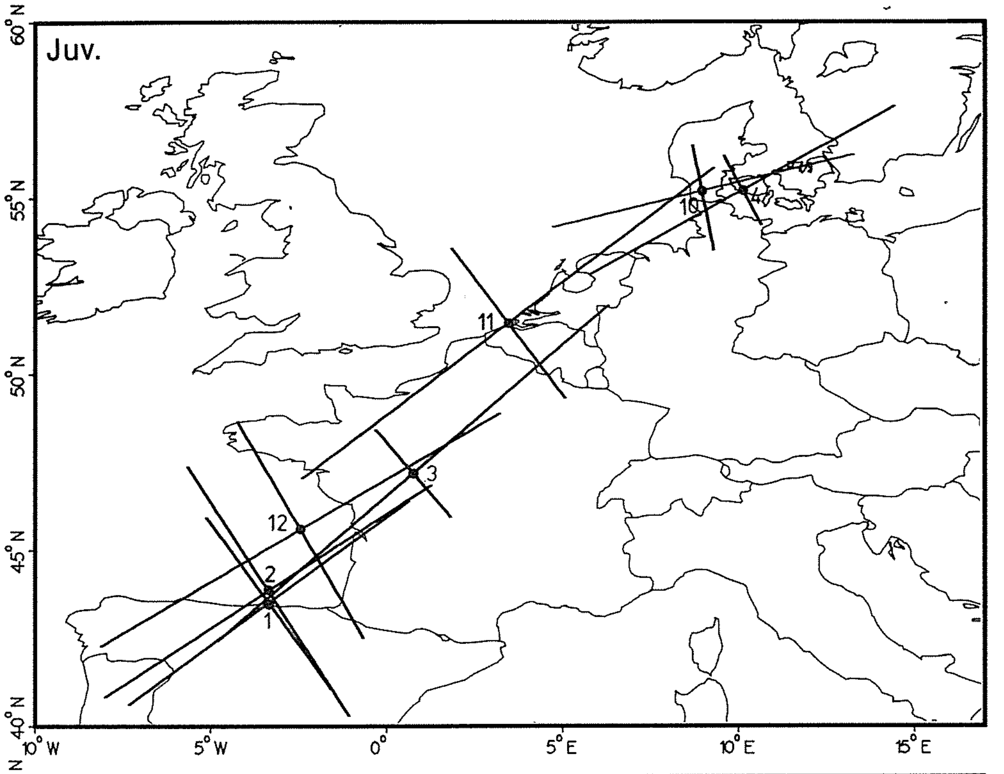
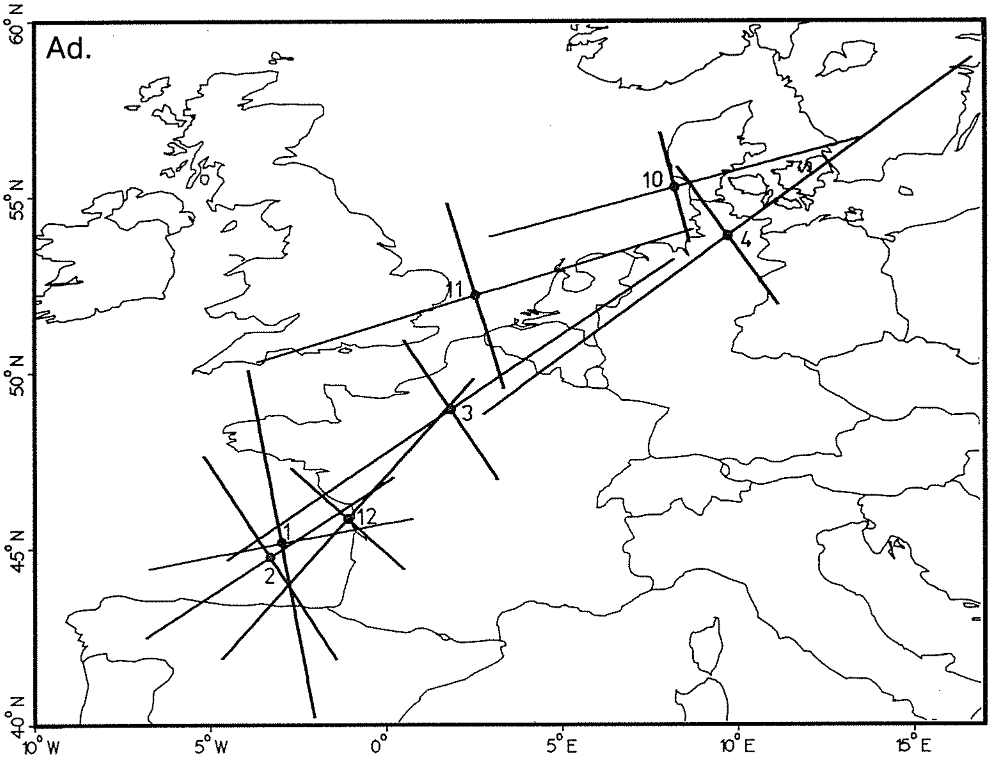


Fig. 5. RR-distance in relation to date of recovery of Lapwings.


Juv.
60° N
55° N
50° N
45° N
40° N
10° W
5° W
0°
5° E
10° E
15° E
1
2
3
4
10
11
12


Ad.
60° N
55° N
50° N
45° N
40° N
10° W
5° W
0°
5° E
10° E
15° E
1
2
3
4
10
11
12

cannot be assumed to originate from a geographically normally distributed population, simpler parametric tests such as the t-test and F-test cannot be used.

Each age-group was further divided into four groups according to the RR-distance (< 100 km, 101-500 km, 501-1,000 km, and > 1,000 km), for the months October-March. A X^2-test showed no significant difference in the distribution of the two age-groups ($p > 0.05$).

However, although the RR-distances were not significantly different in the two groups, there may well be differences in their whereabouts, as the direction may be different.

Using the Kolmogorov-Smirnov two-sample test (SIEGEL 1956), no significant difference ($p > 0.05$) was found between the two age-groups in a comparison of the monthly latitude and longitude coordinates of recoveries. This was not in any case expected, following a direct comparison of the two maps in Fig. 6.

From the data then, it can be concluded that there are no significant differences in the migration patterns of juvenile and adult Lapwings. It should however be borne in mind that for some months of the year only relatively few recoveries exist, and thus further recoveries may lead to an alteration of this conclusion.

Migratory movements in summer

Movements of Lapwings during the summer have often been described, e.g. SCHÜZ (1932), DAANJE (1935), PUTZIG (1938), KRAAK et al. (1940), KLOMP (1946), LACK (1962), NIETHAMMER (1970), BESER (1972) and SALOMONSEN (1972). Terms such as interim movements (Zwischenzug), early summer migration (Frühwegzug), moult migration and juvenile migration have all been used; however there is some confusion as regards the definition of these different phenomena (e.g. see PUTZIG 1938 and VON SCHWEPPENBURG 1942). As different authors apparently often used the above terms as synonyms, and it is not possible to distinguish different types of migration from individual recoveries, the term summer migration will be used in this account.

SALOMONSEN (1946 & 1972) states that it is common for juvenile Lapwings to migrate in a southerly direction, as early as May, June and July. In order to verify this statement, juveniles recovered before August 1st in the year of ringing have been analysed. Out of 84 recoveries in this category 70 (83%) have been found at the ringing site, another 13 (3 from June and 10 from July) were recovered between 2 and 20 km from the ringing site, and the last one was found on July 2nd on a fishing-boat in the North Sea, 370 km from the ringing site (Table 5). From this information, no indications of a juvenile migration can be concluded. From ringing data it is known that the number of 1-2 week-old chicks in Denmark reaches a peak around June 1st (BAK & ETTRUP, in prep.). Therefore the majority is not fully-fledged until July, and thus a juvenile migration cannot occur until after this time.

During July-September, 196 juvenile Lapwings were recovered (Table 2). However, of the recoveries from July, 5 were from the year following ringing, due to the age-grouping system chosen. Of the re-

Fig. 6. Monthly mean coordinates and standard deviations of recoveries of Danish Lapwings during October-April.

RR-distance km	0-1	2-5	6-10	11-20	370
No. recovered	70	2	6	5	1

Table 5. RR-distance of 84 Lapwings ringed as chicks and recovered during May-July in year of ringing.

RR-distance km	Juv. Jul. No.	Juv. Aug. No.	Juv. Sep. No.	Juv. Total No.	Juv. Total %	Ad. Jul. No.	Ad. Aug. No.	Ad. Sep. No.	Ad. Total No.	Ad. Total %
0	25	54	20	99	*52*	2	21	14	37	*43*
1-10	6	14	1	21	*11*	–	6	9	15	*17*
11-20	4	20	7	31	*16*	–	7	2	9	*10*
21-100	–	14	14	28	*15*	1	8	7	16	*19*
> 100	1	7	4	12	*6*	2	4	3	9	*10*
Total	36	109	46	191	*100*	5	46	35	86	*99*

Table 6. RR-distance of juvenile and adult Lapwings recovered during July-September.

maining 191, 120 (63%) were recovered less than 10 km from the ringing site, and only in 12 cases (6%) was the RR-distance more than 100 km (Table 6). The predominant migration routes for these 12 birds were in southerly and westerly directions, indicating that the juvenile migration can be considered as a forerunner of the actual migration.

Comparison with adult Lapwings from the same period (Table 6) shows that 52 (60%) are recovered less than 10 km from the ringing site, while only 9 (10%) have an RR-distance of more than 100 km; however some of the latter are probably abmigrated birds (see p. 14). A X^2-test also suggests there is no significant difference ($p > 0.05$) in the RR-distance of the two age-groups, indicating that summer migration in the Danish Lapwing population is neither a distinct juvenile nor adult phenomenon, but occurs in both age-groups.

Although perhaps only a small proportion of the population takes part in this migration, the term "early summer migration" (Frühwegzug) (Putzig 1938) is believed to be the best one for this phenomenon, whether it concerns a moult migration, or whether it is a dispersal mechanism to avoid food competition.

However, from the present recoveries alone it is difficult to show more large-scale movements during summer, but this may possibly more be due to an insufficiency of recoveries rather than to the real situation. Lack (1962) has for instance shown, from radar observations and field studies, that migratory activity in Lapwings across the North Sea takes place in summer.

Homing and abmigration

Migratory birds generally return to their place of birth to breed (Edelstam & Österlöf 1969). For the Woodcock *(Scolopax rusticola)*, Alexander (1946) found that about 88% of the British population returned to the place of birth, and Soikkeli (1970) found that all Dunlin *(Calidris alpina)* from a study area in Finland returned to the place of birth.

Lapwings, however, show less attachment to a particular place. Of 135 Danish chicks ringed and all recovered during April-July in subsequent years, 73 (54%) were found less than 10 km from the ringing site, and 62% of the birds were recovered inside 20 km from the ringing site (Table 7). Lapwings in Denmark appear less attached to their place of birth than those in Norway, where Grimeland (1966) found 68% less than 10 km from the ringing site, and those in Holland, where Kraak et al. (1940) found 72%. Imboden

RR-distance km	Juv. No.	Ad. No.	Total No.
0-1	28	36	64
2-5	1	1	2
6-10	2	5	7
11-20	5	6	11
21-50	3	9	12
51-200	4	11	15
201-500	3	6	9
501-1000	2	4	6
> 1000	2	7	9
Total	50	85	135

Table 7. RR-distance of 135 Lapwings (including 22 controls) ringed as chicks in Denmark and recovered during April-July the following years. Juveniles were recovered in calendar year after ringing, adults in the next and subsequent years.

(1974), who set a limit of 20 km for place attachment, found that about 70% of the European Lapwings returned to the place of birth.

Some Lapwings are recovered in summer far from their place of birth (Table 7). Such birds are considered to have abmigrated, even although it is naturally not possible for an individual recovery to decide whether that particular bird bred in the new area or was only resting there temporarily (oversummering juvenile, bird on summer migration, etc.). In Fig. 7, the place of recovery of 34 birds ringed in Denmark as chicks and recovered abroad in subsequent years during the breeding period April-July, is shown. Furthermore, another 3 recoveries from March, 1 from August and 1 from September are included, as they were found in areas north and east of Denmark, and should thus be considered as abmigrated birds. Of the recoveries from April, 3 from West Germany and 1 from Holland may derive from birds still on spring migration. It is seen that Lapwings from Denmark in particular find new breeding areas along migration routes and in winter quarters, but also in areas north and east of Denmark. The limits are represented by 2 birds from

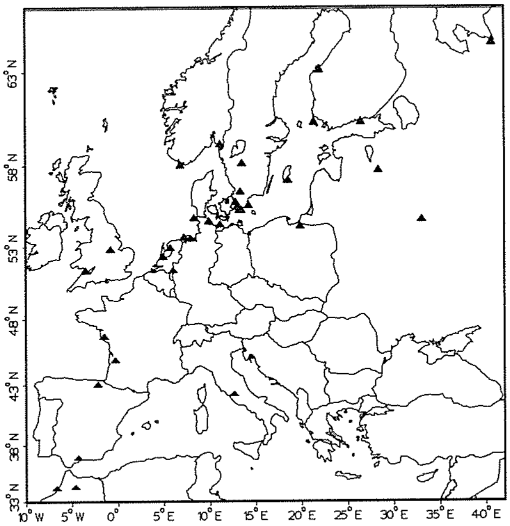


Fig. 7. Geographical distribution of 34 Lapwings ringed as chicks in Denmark and recovered abroad, during April-July.

Country of recovery	Month of recovery Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Total
U.S.S.R.	-	-	-	1	1	2	-	1	-	-	-	-	5
Finland	-	1	-	1	10	17	7	3	-	-	-	-	39
Sweden	-	2	4	5	41	33	22	9	5	-	-	-	121
Norway	3	1	1	3	20	10	10	7	1	-	1	3	60
W. Germany	3	1	1	1	3	2	1	-	-	1	-	-	13
Holland	1	-	-	-	1	3	-	-	-	-	-	-	5
British Isles	1	1	-	1	-	-	-	-	-	-	-	-	3
Total	8	6	6	12	76	67	40	20	6	1	1	3	246

Table 8. Recoveries of 246 Lapwings ringed as chicks abroad and later recovered in Denmark.

Morocco, 2 and 11 years old, recovered approximately 2,700 km south-west of the ringing site, and 2 from the U.S.S.R., 2 and 3 years old, recovered 1,800 and 1,400 km respectively east of Denmark. Of special interest is a recovery of a 10-month old Lapwing from Italy in May. This bird was found outside the flyways normally followed by the Danish population.

On the other hand, Lapwings from other populations also abmigrate to Denmark, as indicated by ringing recoveries (Table 8). Of these, 32 are from the breeding period of April-July, 5 from the year of ringing and 27 from subsequent years. It is interesting to see that the geographical distribution of the ringing areas of the latter 27 recoveries (Fig. 8), shows the same pattern as that found in abmigrated Lapwings from Denmark. In particular, it is birds annually passing Denmark on migration which settle here. But in addition, Lapwings from Great Britain, Holland and West Germany settle in Denmark. Furthermore, it is possible that some of the Lapwings recovered during August-March have bred in Denmark, but this cannot be proved.

The intermixing which occurs in the winter quarters and the subsequent abmigration of the different populations provides a lasting gene flow, which in spite of the wide Palaearctic distribution of the Lapwing, prevents any tendency towards a subspecific differentiation (MEAD et al. 1968).

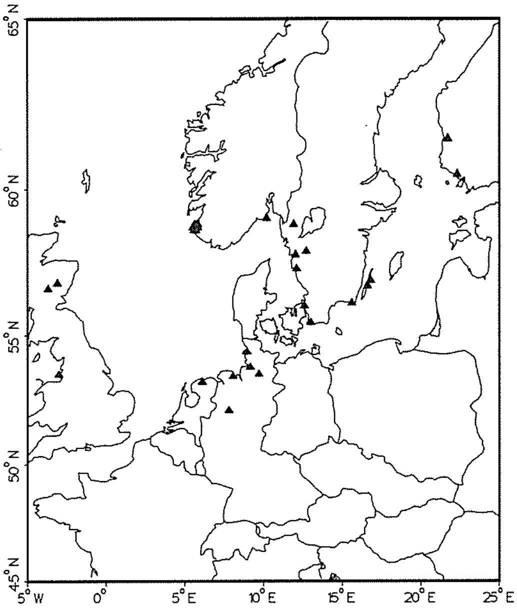


Fig. 8. Site of ringing of 27 Lapwings ringed as chicks abroad, and subsequently recovered in Denmark during April-July.

Mortality

First-year mortality was calculated from recoveries of Lapwings found between August 1st and March 31st in the first year of life. Recoveries occurring prior to August 1st in the year of ringing were excluded due to lack of knowledge of the probability of recovery of non-fledged individuals. During the period August 1st-March 31st, 404 juvenile birds were recovered (Table 9). Excluding the 84 recoveries occurring prior to August 1st, the 404 recoveries comprise 43.9% of the total number of recoveries. GLUTZ et al. (1975) found for the same period a mortality rate of 39.7% for the European population as a whole.

The mean annual mortality for adult Lapwings is presumed to be the same for

Period of recovery	Total
Between ringing and August 1, the same year	84
August 1-December 31 in year of ringing	271
January 1-March 31 in year after ringing	133
After March 31 in year after ringing	517
Total	1005

Table 9. Recoveries of Lapwings ringed as chicks arranged into four age-classes.

Age-class	No. recovered	Age-class	No. recovered
1	241	10	4
2	135	11	4
3	81	12	4
4	61	13	3
5	46	14	1
6	24	23	1
7	28	24	1
8	9		
9	7	Total	650

Table 10. Recoveries of Lapwings arranged in age-classes according to calendar year.

all age-classes, as a X^2-test revealed no significant difference ($p > 0.05$) in the observed and expected distribution of the recoveries, divided into age-classes according to calendar year (Table 10). BOTKIN & MILLER (1974) emphasize however that an assumption of constant adult mortality rate is not always correct. Analyses have shown that species with low annual mortality calculated according to the methods of LACK (1951) and HALDANE (1953 & 1955) reach an unrealistically high age. The fact that this problem has not been evident until now is mainly due to calculations of mortality being applied to species with a rapid population turnover. In such species, the increased mortality with age is not recorded. Using the methods just mentioned, the mean annual mortality is calculated as 33.2 ± 1.1%.

GLUTZ et al. (1975) state the adult mortality of the European population as being 32.2%, without finding significant differences in the populations of different countries. KRAAK et al. (1940) calculated mortality for Lapwings in Holland to be 40 ± 2%. This result is however not directly comparable with the value calculated here, as a different and less refined method of calculation was employed. HALDANE (1955) found an annual adult mortality in British Lapwings of 34.4 ± 1.06%, which is not significantly different from that in the Danish population ($p > 0.05$). This seems surprising, as migratory populations generally show greater mortality than sedentary ones. MURTON (1971) states that the difference in mortality between Lapwings in Britain and Holland is due to the very fact that Lapwings in Britain are sedentary, while those in Holland are migratory. The same conclusion is reached by CLAUSAGER (1974) in a study of Woodcock. The present study can thus not support this assumption, but it is possible that other, more complex factors may influence.

From the calculated mortalities and according to LACK (1954) and FOG (1964) the mean life expectancy for juvenile Lapwings is calculated to approximately 2 years 1 month, while adults can expect to survive 2 years 6 months.

As a point of interest, the present material contained records of 3 Lapwings more than 20 years old. Two were ringed in Denmark as chicks (May 21st 1948 and May 21st 1940) and recovered at ages of 22 years 8 months and 24 years 7 months respectively (January 20th 1971 and December 13th 1964). These exceed earlier maximum ages given by RYDZEWSKI (1978) of just over 23 years 2 months. The record however belongs to a Lapwing ringed in Holland on March 20th 1939. At the time of ringing it was more than 6 months old, and was thus at least 25 years old, when recovered on September 9th 1963 in West Jutland.

If the Danish Lapwing population is to be maintained at a stable level, the number of adults which die in a year must be balanced by the number of juveniles which survive until the next breeding season. It is supposed that emigration and immigration are of a similar order, and thus have no influence in this connection. It is furthermore stated that Lapwings are mature in their first breeding season. Calculations of the mortality rate indicate that of 100 adults birds, 33 die before the next season. These must therefore be replaced by a similar number of juveniles. Since the first-year mortality rate is 43.9%, this means that 100 adults must produce 59 fledglings alive on August 1st. This corresponds to a ratio of 1.18 juveniles per pair starting the breeding season.

Studies of the breeding success undertaken at different habitats in Denmark during 1978-79 (BAK & ETTRUP, in prep.). show that the production of 1.18 juveniles per breeding pair is not unrealistic. For instance, in an area comprised of arable land and fields which supported a rather low density of pairs, a minimum production of 0.57 juveniles per pair was found, whilst the production in wet coastal grassland which supported the most dense populations was calculated to be at minimum 1.24 juveniles per pair.

On the basis of the mortality figures given by GLUTZ et al. (1975), a similar juvenile production necessary to sustain the total European population is calculated to be 1.07 juveniles per pair present at the start of the breeding season. LACK (1943) found for the British Lapwing population that 1.06 juveniles must be produced per pair.

Dansk Resumé

Danske vibers *(Vanellus vanellus)* trækforhold og dødelighed

Til brug for en analyse af danske vibers træk- og omsætningsforhold er der indsamlet 1085 genmeldinger af fugle mærket som unger i årene 1920-78 (Tabel 1). Genmeldingsprocenten er beregnet til 4,7.

Materialet er opdelt i juvenile, der omfatter fugle genmeldt inden 1. august året efter mærkningen, og adulte, der består af fugle genmeldt senere end 31. juli året efter mærkningen. Juvenilgruppen kan med denne opdeling indeholde individer, som ifølge sædvanlig definition ikke længere er juvenile.

Til bearbejdning af de indsamlede data er anvendt EDB, hvorved det er muligt på kort tid at fremstille dels plotkort, som viser de enkelte genmeldingers geografiske fordeling, dels oversigtskort, der ved gennemsnitskoordinater og standardafvigelser viser populationens hovedudbredelse i bestemte tidsrum. Sidstnævnte udarbejdes ved ud fra koordinaterne for en periodes genmeldinger først at beregne disses regressionslinie. Den kan i trækperioden tages som udtryk for populationens bevægelsesretning. Dernæst drejes og forskydes det traditionelle, geografiske koordinationssystem, hvor x-aksen er ækvator og y-aksen 0°-længde (Greenwich). Herved føres x-aksen over i regressionslinien, og standardafvigelserne i dennes retning og vinkelret herpå udregnes i det nye koordinatsystem (Fig. 2). Disse beregninger foretages uafhængigt fra periode til periode. Anvendelsen af denne metode illustrerer vibepopulationens udbredelse bedre, end hvis tilsvarende beregninger foretages i det oprindelige koordinatsystem (Fig. 1).

Den geografiske fordeling af genmeldingerne fremgår af Tabel 2 og 3, mens Fig. 3 og 4 viser de eksakte genmeldingssteder i perioden oktober-april.

Efterårstrækket, der indledes midt i oktober, forløber fortrinsvis over Storbritannien. Vinterkvartererne, der strækker sig fra Storbritannien til den Iberiske Halvø og Nordafrika, nås i løbet af december (Fig. 5). Enkelte viber forbliver i milde vintre i Danmark. Der er en tendens til, at de juvenile trækker længere sydpå end de adulte fugle, idet RR-afstanden (afstanden mellem mærkningssted og genmeldingssted) i gennemsnit er 100-150 km større hos de juvenile. Forårstrækket starter sidst i februar - begyndelsen af marts, og i løbet af april er viberne tilbage på ynglepladserne.

Oversigtskortene (Fig. 6) viser, at der ved såvel efterårs- som forårstrækket er en stor standardafvigelse i trækretningen, og lille vinkelret på denne. Afvigelserne bliver mere ens i begge retninger, når fuglene har nået vinterkvartererne. Det vestorienterede efterårstræk og det mere østligt forløbende forårstræk ses ligeledes.

Undersøgelse af trækaktiviteten i sommerperioden viser, at trækket af juvenile endnu ikke er begyndt ved udgangen af juli, idet ca. 99% endnu befinder sig inden for en afstand af 20 km fra mærkningsstedet (Tabel 5). Med udgangen af september er flere påbegyndt vandringen, og ca. 6% findes nu mere end 100 km fra mærkningsstedet (Tabel 6). Fordelingen af genmeldte adulte viber afviger ikke signifikant fra de juveniles fordeling. Sommertrækket er således ikke kun et fænomen, der forekommer blandt juvenile, men må betragtes som et tidligt borttræk, hvori såvel juvenile som adulte deltager.

I den danske vibepopulation vender 62% tilbage til klækningsområdet for at yngle inden for 20 km fra mærkningsstedet (Tabel 7). Det er en mindre andel, end der er påvist hos norske og hollandske viber .

Nogle danske viber udvandrer til andre lande (Fig. 7). Genmeldingerne viser, at det fortrinsvis er til lande, som besøges i vinterhalvåret. Men også til lande,

der ligger uden for trækruterne (nord og øst for Danmark) sker der en udvandring. Tilsvarende indvandrer også udenlandske viber til Danmark. Blandt 246 viber mærket i udlandet som unger og genmeldt i Danmark er således de 27 fra yngleperioden april-juli (Tabel 8 og Fig. 8).

Førsteårsdødeligheden i perioden 1. august-31. marts er beregnet til 43,9%, og den forventede yderligere levetid til 2 år 1 måned. Den gennemsnitlige årlige dødelighed for adulte viber er beregnet til 33,2 ± 1,1% og den forventede yderligere levetid til 2 år 6 måneder. Den adulte dødelighed afviger ikke fra, hvad der er fundet i andre europæiske bestande. Viber kan nå en betydelig alder, og de to ældste i det foreliggende materiale blev henholdsvis 22 år 8 måneder og 24 år 7 måneder. Rekorden har imidlertid en hollandsk mærket vibe, der ved sin død var mindst 25 år.

Såfremt der skal være balance i den danske vibebestand, skal hvert par, der påbegynder ynglesæsonen, i gennemsnit producere 1,18 flyvedygtig unge. Dette er heller ikke urealistisk, idet der på de bedre danske strandenge er registreret en produktion på mindst 1,24 unge pr. par.

Резюме на русском языке

Условия миграции и смертность датских чибисов *(Vanellus vanellus)*

Для анализа условий миграции и оборота чибисов было собрано 1085 сообщений о встречах птиц, помеченных будучи птенцами в периоде с 1920 по 1978 г. (Табл. I). Вычисленный процент возвратов - 4,7%.

Материал подразделен на молодых, включающих птиц, о которых получены сообщения до I августа года после их пометки, и взрослых, включающих птиц, о которых возвраты датированы позднее 3I июля года после пометки. При таком подразделении группа молодых может содержать особей, по обычному подразделению уже не считающихся молодыми.

Для обработки собранных данных применялась ЭВМ, что позволяет быстрое изготовление как карт с нанесенным географическим распределением отдельных возвратов, так и обзорных карт, при помощи средних координат и стандартных отклонений показывающих основное распределение популяции в определенных периодах. Последние разрабатываются, из координат возвратов данного периода сначала вычисляя их линию регрессии. В периоде перелета её можно считать указанием о направлении передвижения популяции. Затем традиционную географическую систему координат, осью x которой служит экватор, а осью y – нулевой меридиан (Гринича), поворачивают и сдвигают. Этим ось x переносится на линию регрессии, и стандартные отклонения в её направлении и перпендикулярно к ней вычисляются по отношению к новой системе координатных осей (фиг. 2). Эти вычисления независимо одно от другого производятся с периода на другой. Применением этого способа распространение популяции чибисов иллюстрируется лучше, чем соответствующими вычислениями в первоначальной системе координат (фиг. I).

Географическое распределение возвратов показано в Табл. 2 и 3, а фиг. 3 и 4 показывают точное расположение мест, из которых получены возвраты в периоде с октября по апрель.

Осенний перелет, начинающийся в середине октября, в общем проходит через Великобританию. На места зимовки, распространенные от Великобритании до Пиренейского Полуострова и Северной Африки, птицы прибывают в течение декабря (фиг. 5). Немногие чибисы в мягкие зимы остаются в Дании. Замечается тенденция к тому, что молодые мигрируют дальше на юг, чем взрослые птицы, так как расстояние RR (от места пометки до места, из которого получен возврат) у молодых в общем на 100-150 км дальше. Весенний перелет начинается в конце февраля – начале марта, и в течение апреля чибисы возвращаются к местам гнездования.

Обзорные карты (фиг. 6) показывают, что как при осеннем, так и при весеннем перелетах стандартное отклонение в направлении перелета значительно, а в перпендикулярном к нему направлении невелико. Отклонения в обоих направлениях становятся более равными когда птицы прибыли в местности зимовки. Показаны также ориентированный на запад осенний, и проходящий восточнее его весенний перелеты.

Исследования перелетной деятельности во время летнего периода показывают, что перелет молодых в конце июля еще не начался, так как прибл. 99% из них еще находятся на расстоянии не дальше чем 20 км от места пометки (Табл. 5). До конца сентября более значительное число их начало миграцию, и прибл. 6% теперь встречаются дальше чем 100 км от места пометки (Табл. 6). Распределение взрослых чибисов, о которых получены возвраты, только незначительно отличается от распределения молодых. Следовательно, летний перелет следует рассматривать не как явление, особенное для молодых, а как ранний отлет с участием как молодых, так и взрослых.

Из датской популяции чибисов 62% возвращаются в местность выводки и гнездуют не дальше чем 20 км от места пометки (Табл. 7). Эта доля меньше обнаруженной у норвежских и голландских чибисов.

Некоторые датские чибисы эмигрируют в другие страны (фиг. 7). Возвраты показывают, что это главным образом те-же страны, которые они пóсещают в зимнем полугодии. Однако, происходит также эмиграция в страны, расположеные вне путей перелета (к северу и к востоку от Дании). Соответственно с этим в Данию иммигрируют и иностранные чибисы. Из 246 чибисов, помеченных будучи птенцами заграницей, и о которых получены сообщения о встречах в Дании, имеются 27 из периода выводки с апреля по июль (Табл. 8 и фиг. 8).

Первогодная смертность за период с I августа по 3I марта по вычислению составляет 43,9%, а ожидаемая продолжительность дальнейшей жизни 2 г. I месяц. Средняя годовая смертность взрослых чибисов по вычислению составляет 33,2 ± I,I%, а ожидаемая продолжительность дальнейшей жизни 2 г. 6 месяцев. Смертность взрослых не отличается от констатированной у других европейских популяций. Чибисы могут достичь значительной старости: двум старейшим особям в имеющемся в распоряжении материале было соответственно 22 года 8 месяцев и 24 года 7 месяцев. Однако, рекорд держит чибис, помеченный в Голландии, которому при его смерти было по меньшей мере 25 лет.

Для поддержания баланса датской популяции чибисов, каждая пара, начинающая сезон гнездования, должна вырастить средним числом I,I8 способного летать птенца. Это вполне реалистично, так как на лучших из прибрежных лугов Дании зарегистрирована продукция, соответствующая I,24 птенцам на пару.

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