Rohrsängern. Anz. Orn. Ges. Bayern 5: 389-433 • Stewart, R. E., & J. W Aldrich (1951): Removal and repopulation of breeding birds in a spruce-fir forest community. Auk 68: 471—482 • Svensson, S. E. (1978): Territorial exclusion of Acrocephalus schoenobaenus by A. scirpaceus in reedbeds. Oikos 30: 467—474 ● Szabó, L. V. (1973—74): Das Brüten des Seggenrohrsängers (Acrocephalus paludicola) in der Hortobágy. Aquila 80-81: 41-53 • Thévenot, M., & P. Thouy (1974): Nidification au hivernage d'especes peu connues ou nouvelles pour le Maroc. Alauda 42: 51-56 ● Thompson, Ch. F. (1977): Experimental removal and replacement of territorial male yellow-breasted chats. Auk 94: 107—113 • Tinbergen, N., M. Impekoven, & D. Franck (1967): An experiment on spacing-out as a defence against predation. Behaviour 28: 307—321 ● Tree, A. J. (1966): Notes on the Palaearctic migrants in the North Kafue basin, Zambia. Ostrich 37: 184-190 • Ders. (1971): Notes on Palaearctic migrants in the eastern Cape. Ostrich 42: 198-204. Udvardy, M. D. F. von (1958): Ecological and distributional analysis of North American birds. Condor 60: 50-66 • Ursprung, J. (1980): Interspezifische Territorialität bei Rohrsängern - Fragestellung, Methodik und erste Ergebnisse einer laufenden Untersuchung am Neusiedlersee. Biol. Forsch. Inst. Burgenland Ber. 37: 67—71 ● Verheyen, R. (1953): Oiseaux — Exploration du Parc National de l'Upemba. Mission G. F. de Witte. Fasc. 19 Inst. nat. Park. Belg. Congo, Bruxelles • Walter, H. (1978): Ökologie der Sylviiden. Abstracts, Symposia and Special Interest Groups XVII Congr. Intern. Orn. 94 • Watson, A. (1964): Aggression and population regulation in Red grouse. Nature 202: 506—507 ● Ders. (1967): Territory and population regulation in the Red grouse. Nature 215: 1274—1275 • Watson, A., & D. Jenkins (1968): Experiments on population control by territorial behaviour in the Red grouse. J. Anim. Ecol. 37: 595-614. • Weisser, P. (1970): Die Vegetationsverhältnisse des Neusiedlersees. Wiss. Arb. Burgenland 45: 83 S. Whitmore, R. C. (1977): Habitat partitioning in a community of passerine birds. Wils. Bull. 89: 253-265 • Ders. (1979): Temporal variation in the selected habitats of a guild of grassland sparrows. Wilson Bull. 91: 592— 598 • Whittaker, R. H. (1975): Communities and Ecosystems. MacMillan, New York • Wiens, J. A. (1969): An approach to the study of ecological relationships among grassland birds. Orn. Monogr. No. 8 ● Willson, M. F. (1966): Breeding ecology of the Yellow headed Blackbird. Ecol. Monogr. 36: 51—77 ● Zahavi, A. (1957): The breeding birds of the Huleh swamp and lake (Northern Israel). Ibis 99: 600—607 ▼ Zink, G. (1973): Der Zug europäischer Singvögel. 1. Lieferung, Radolfzell

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The migration of European Sandwich Terns Sterna s. sandvicensis. I

By Anders Pape Moller

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1. Introduction

The Sandwich Tern breeds at high density in large colonies which have been visited by ringers for decades. Therefore, a large number of nestlings has been ringed. Disturbance of breeding colonies, catching of birds for food in the winter range, and the increasing catches of fish by man along the migration routes and in the winter quarters of the Sandwich Tern are some of the factors affecting numbers.

Studies of migration have been made both for populations from different countries (Thomson 1943, Schloss 1966, Langham 1971, Rosendahl & Skovgaard 1971, Elliot 1971, Isenmann 1972, Ardamatskaya 1977, Campredon 1977) and for the entire population of the European range (Müller 1959), but these investigations are all more or less restricted in their scope, as the aims have been rather specific. Therefore, a comparative investigation of the entire European population is desirable. Furthermore, as Sandwich Terns change breeding site very often, sometimes moving large distances (Nehls 1969), it would be interesting to know if European Sandwich Terns behave as a single population or many separate ones from a migrational point of view.

Only the migrational aspects of the biology of the species will be dealt with here. Mortality rates, causes of death and changes in breeding sites will be considered elsewhere.

2. Acknowledgements

First and foremost I would like to thank the many ringers who have ringed more than 200000 Sandwich Terns during the present century. Without their effort this investigation would have been impossible.

B. J. Speek, Arnhem has given me access through Euring to a huge number of recoveries. Furthermore I would like to thank S. ÖSTERLÖF, Sweden, N. O. PREUSS, Denmark, A. SIEFKE, GDR, H. ROGALL, FRG, B. J. Speek, Netherlands, R. Spencer, Great Britain and J. Backstrom, France for giving me permission to use the recoveries from their respective countries and for various kinds of help. R. Lambert, Alford, M. Sutherland, Sandwich, N. Riddiford, Romney Marsh, P. Jennings, Calf of Man, J. Cudworth, Ossett, M. Rogers, Portland, H. Holgersen, Stavanger, J. Fahlberg and H. Meltofte, Copenhagen and D. Moritz, Wilhelmshaven-Rüstersiel are all thanked for giving me permission to use records from various bird observatories in northern Europe. E. Flensted-Jensen, Ø Brønderslev and B. J. Speek, Arnhem are thanked for giving me a large number of old rings from Copenhagen and Arnhem. C. Mead, Tring is thanked for help and discussions. The Scientific Committee of the Danish Ornithological Society has offered economic help for a journey to Great Britain, C. Lloyd, Dublin has kindly corrected the paper linguistically and suggested a number of improvements. E. K. Dunn, Oxford suggested various alterations.

3. Ringing

Within the northern European range of the Sandwich Tern, 214.572 birds have been ringed, and 4915 recoveries have been reported (Table 1); 4725 recoveries from Denmark, West Germany, Netherlands and Great Britain and Ireland have been used here. The migration of the Sandwich Tern populations of other European countries is discussed briefly. Recovery rates range from 1.07% in Hiddensee rings to 3.04% in Arnhem rings (Table 1). However, the recovery rates cannot be compared as Sandwich Terns have been ringed in Sweden and GDR only for a couple of decades, whereas the other ringing centres have ringed terns since the beginning of the present century. It is a possibility, that the "unknown" address of Viborg rings has reduced the recovery rate, as Copenhagen rings have a recovery rate of 2.41% compared to only 1.61% for Viborg rings, although the birds have been ringed within the same areas. A final conclusion cannot be put forward, as the Viborg rings were used mainly in the 1920's and 1930's, whilst the Copenhagen rings have been used in the later decades. Finally, the metal from which rings were made has to be considered. Early rings were generally made of soft alloys, and therefore they often wore badly. The

Table 1: Number of Sandwich Terns ringed and recovered by the main European ringing schemes. Years indicate the last year to which records are taken for this study.

Ringing centre	No. of birds ringed	Year	No. of birds recovered	Recovery rate (%)
Stockholm	8654	1975	126	1.46
Copenhagen	26895	1975	647	2.41
Viborg	16634	1971	267	1.61
Hiddensee	6000	1976	64	1.07
Helgoland	43175	1978	1002	2.32
Arnhem	19574	1975	595	3.04
London	93640	1975	2214	2.36
Total	214572		4915	2.29

number of recoveries from the beginning of the century may have been highly reduced lowering the recovery rates.

The numbers of Sandwich Terns ringed and recovered in their first year of life for Denmark, West Germany, Netherlands and Great Britain and Ireland show that the ringing effort and thereby the number of recoveries has increased during the later years (Table 2). The temporal distribution of the ringing effort is therefore biased towards the late 1960's and early 1970's.

Table 2: The number of Sandwich Terns ringed and those recovered in their first year of life in four European countries.

Period	Denn	Denmark		West Germany		Netherlands		Ireland, Great Britain	
1941—45	1105	6	495	10	256	0	362	1	
1946—50	1367	4	1538	48	701	11	3390	19	
195155	285	4	1539	48	1599	28	5194	58	
1956—60	1664	7	4413	118	1 <i>7</i> 15	28	10105	109	
1961—65	4172	15	6432	277	2805	100	16834	202	
1966— <i>7</i> 0	7190	66	6336	78	3156	33	21213	373	
1971—75	6697	49	12739	182	9342	1111	18359	253	

It has been shown several times that ring wear plays an important role when analysing recoveries of long-lived bird species. Rings may already be unreadable after 8—10 years on a bird, but rings usually remain legible for 10 years (A. P. Møller, unpubl.). Ring wear is discussed in more detail elsewhere (A. P. Møller, in prep.). As the recoveries have been split up in three age categories, the oldest being 4y+ birds (birds four years or older), I have not found any reason to consider ring wear in the present connection.

4. Methods

Distances covered by recovered birds have been calculated according to the loxodromic formula (IMBODEN & IMBODEN 1972). Errors due to the formula are at a maximum (7—8%) for large distances and considerably smaller for distances less than 600 km.

I have assumed that dispersal is due to random movements (although it may be questioned) of the population and have used the procedure of COULSON & BRAZENDALE (1968). Dispersal rates have been calculated using the formula

 $\mathbf{r} = \frac{\mathbf{N}}{\sum_{j} \cdot \mathbf{p_j}},$

where N is the number of individuals, j is the distance class from the colony and p_j is the number of birds in this class. The standard deviation has been calculated using the formula

$$sd(r) = r \left(\frac{1-r}{N}\right)^{\frac{1}{2}}$$

where r is the dispersal rate and N is the number of birds.

Migration speeds have been calculated only for the months June—December for birds in their first year of life (ly). By December the birds have reached their winter quarters, and further calculations are therefore meaningless. The distances covered by the birds have been divided by the number of days elapsed since ringing. The large amount of data minimises the effect of errors in these calculations. Furthermore comparisons between different areas are especially useful. I have found it most useful to

calculate median values of migration distances instead of mean values, because at any one time some birds may be in the winter quarters (e. g. Angola) and others near the breeding grounds in Europe. Using the mean instead of the median, extreme recoveries will play a far too important role compared to the large number of recoveries elsewhere.

Migration directions have been used several times elsewhere in the analysis of the spatial distribution of recoveries. The Sandwich Tern follows the coast of the eastern Atlantic in Europe and Africa, and the species is found nearly exclusively at coasts. Therefore, migration directions are not discussed here. As most migration probably follows the coasts of the eastern Atlantic, the distances covered by birds may be longer than the distances measured. The calculated distances have not been corrected for this error.

Recoveries are divided into three age classes, viz. ly (birds in their first year of life until 31 May the following year after ringing), 2—3y (immatures in their second and third year from 1 June the year after ringing to 31 May three years after ringing) and 4y+ (adults from 1 June three years after ringing). These classes have been established because some birds may start breeding when 2y, several birds may start breeding when 3y and most birds breed when 4y or older (Danish Tern Group unpubl.). When analysing the recoveries the following categories have been excluded:

- 1) all retraps at breeding grounds, as these often are due to intensive work in certain places,
- 2) all retraps by ringers. Certain ringing groups have sometimes retrapped large numbers of birds on migration or in the winter quarters,
 - 3) all birds ringed as adults. These recoveries are very few,
 - 4) all recoveries without place specifications.

5. Bias when using recoveries to describe migration

Using ringing recoveries to describe a species' distribution rests upon the assumption that the recoveries match the distribution of live birds. However, a large number of biasing factors may be involved. The chance of a ringed bird being recovered depends, among other things, upon the geomorphology of the coast, the human population density along the coast, the occupation of the population (fishermen and hunters are supposed to find more birds than any others), the level of education in the population, the efficiency of the mail services and other local administrative authorities, political, cultural and other sympathies or otherwise in the local population etc. It is impossible to correct for these factors. In certain areas where large numbers of birds are recovered, it has been shown, that the human population often do not bother to report ringed birds to the ringing centres (PALUDAN 1953). This is the case in certain areas in Africa such as Dakar, Senegal and Accra, Ghana. The restricted number of recoveries, changes in the winter quarters of the tern populations and changes in the educational levels makes it impossible to test this hypothesis. Differences in the density of ringing recoveries within different areas of the coast of Africa (Table 3) can be considered to be due to differences in the human population density. For example, the small recovery rate in Liberia compared to Sierra Leone may be due to a lower human population density in Liberia.

In certain parts of Africa Sandwich Terns are caught for food (Allison 1959, Dunn 1981), and the catching effort in different areas may depend upon factors such as human population density, educational level, laws on game preservation etc.

In the present comparative analysis of different populations I have assumed most of these biases will have lesser importance, and that birds from different populations have the same chance of being recovered in each area.

6. Breeding distribution and population size

The Sandwich Tern has a cosmopolitan world breeding distribution and occurs in the Palearctic region along the central and northern European coasts, and at scattered sites in the western Mediterranean, the Black Sea and the Caspian Sea. In the Nearctic and Neotropical regions the subspecies *acuflavida* is found along the southern Atlantic coasts of USA and the coasts of the Carribean, and in South America south to Rio Grande do Norte, Brazil (Voous 1960, 1977).

A total of c. 41.000 pairs of Sandwich Terns breed within the European range in 1978 (Table 4). Large numbers were found in Denmark, West Germany, Netherlands, Great Britain and France. In the Mediterranean breeding occurs rather irregularly in Italy (Cramp et al. 1974, Toschi 1969), Spain (Maluquer & Pons Oliveras 1961, Cramp et al. 1974) and Tunisia (Castan 1961, Heim de Balsac & Mayaud 1962). Earlier the species was more numerous in Denmark, West Germany and the Netherlands, but lacking in Estonia, Poland,

Table 3: Density of Sandwich Tern ringing recoveries and human population density in the coastal regions of Africa. Recoveries are from Denmark, West Germany, Netherlands and Great Britain and Ireland. Population densities according to Fullard (1970).

Country	Recoveries/100 km coast	Humans/km²
Morocco	2.3	12—25
Rio di Oro	0.3	0—1
Mauritania	7.1	1—3
Senegal	75.6	25—50
Gambia	0.0	2550
Guinea-Bissau	0.0	25—50
Guinea	4.7	25—50
Sierra Leone	44.7	25—50
Liberia	11.6	3—6
Ivory Coast	24.7	12-25
Ghana	84.3	25—50
Togo	12.5	25—50
Benin	8.3	25—50
Nigeria	2.4	25—50
Cameroun	0.2	25—50
Equatorial Guinea	0.0	6—12
Gabon	3.3	3—6
Congo	6.9	25—50
Zaire	0.0	25—50
Angola	11.1	1—3
Namibia	0.9	0—1
South Africa	1.6	25—50

Table 4: Population size of the Sandwich Tern in different countries. Census years are indicated. According to P. H. Becker in litt., H. W. Nehls in litt., E. K. Dunn in litt., E. Flensted-Jensen in litt., G. J. Thomas in litt.

Country	Pairs	Percentage	Year
Estonia	300	0.7	1978
Poland	62	0.2	1978
DDR	1001	2.5	1978
West Germany	7084	17.5	1978
Norway	0	0.0	1978
Sweden	1100	2.7	1978
Denmark	5100	12.6	1978
Netherlands	6100	15.1	1978
Great Britain	11990	29.6	1978
Ireland	1824	4.5	1978
France	5700	14.1	1978
Spain	255	0.6	1979
Italy	7	0.0	1979
Total	40523	100.1	

GDR, Sweden and France outside Brittany (Dybbro 1978, Schulz 1947, Rooth & Mörzer Bruijns 1959, Sof 1978, Nehls 1969, Yeatmann 1976, Tomialojĉ 1972, Aumees & Paakspuu 1963).

7. Investigation areas

It is not possible to divide the European population of Sandwich Terns into sub-populations although retraps of ringed birds at the breeding grounds in Denmark have indicated several sub-populations in the area including the Danish seas. Separate populations are found in West Jutland, Western Limfjord, Northern Kattegat, Southern Kattegat, the

Sound and a part of Scania, the Eastern Baltic etc. (Danish Tern Group, unpubl.). Unfortunately, a comparable number of retraps is not avilable from the other countries. Therefore, the recoveries have been analysed for each country separately. Recoveries from Denmark, FR Germany, Netherlands and Great Britain and Ireland combined are analysed in detail, while recoveries from other countries only are discussed briefly due to their small numbers.

8. Migration behaviour

The Sandwich Tern is a typical diurnal migrant, although it often commenses migration at nightfall. Migration seems to peak during the morning and the evening. Most migration takes place within a few hundred metres of the coast, and the birds only very rarely pass outside the continental shelf. The birds fly just a few metres above the water, usually in small flocks but sometimes up to several hundred birds. Migration can be seen during all types of weather except storms and heavy precipitation.

9. Dispersal

9.1. Post-fledging dispersal

THOMSON (1943) was the first to notice post-fledging dispersal in the Sandwich Tern. He suggested that a marked preference for northward dispersal rather than southward dispersal existed in British birds. MÜLLER (1959) found similar dispersal in Dutch and West German

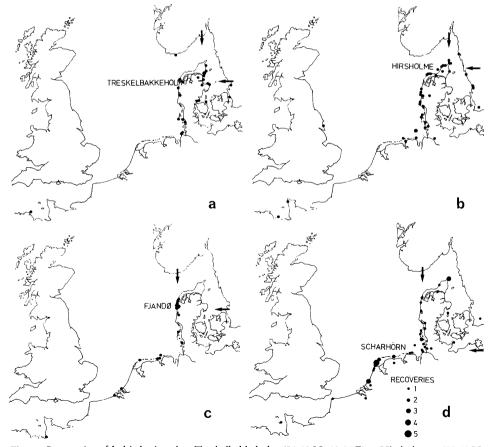


Fig. 1: Recoveries of ly birds ringed at Treskelbakkeholm (56.42 N, 10.15 E) a, Hirsholmene (57.29 N, 10.37 E) b, Fjandø (56.21 N, 08.11 E) c, Denmark, and at Scharhörn (53.58 N, 08.24 E) d, FR Germany from June to September.

birds. Langham (1971) found no prevailing northward dispersal in British Sandwich Terns, and he furthermore suggested, that the birds on a southward dispersal were mixed up with northward dispersing birds on their regular migration towards the winter quarters. Anyhow, it is still possible, that the birds, when migration starts, are moving with a higher speed and therefore passing through the southern dispersal range, leaving only few recoveries.

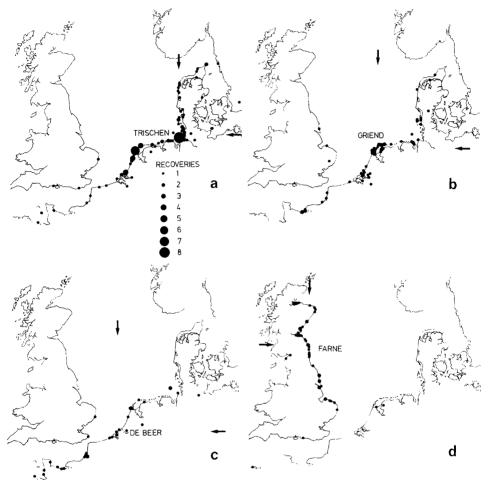


Fig. 2: Recoveries of ly birds ringed at Trischen (54.03 N, 08.32 E) a, FR Germany, Griend (53.18 N, 05.12 E) b, De Beer (51.57 N, 04.07 E) c, Netherlands, and at Farne Islands (55.38 N, 01.37 W) d, Great Britain from June to September.

Dispersal patterns for 8 colonies from which a large number of recoveries are available, are shown in Figs. 1 and 2. Birds from two Danish colonies in Kattegat and one colony in West Jutland near the North Sea are shown in Fig. 1 a, b, c. Birds from Kattegat colonies disperse to Kattegat, Skagerrak and the Wadden Sea, while birds from Fjandø are only found in the North Sea area and keep out of the inner Danish waters. Birds from Trischen and Scharhörn are found especially in the Wadden Sea and on the Danish west coast. Only very few birds are found in Kattegat and the Baltic (Figs. 1d and 2a). Birds from the Dutch colony Griend are found especially in the Wadden Sea and in Zeeland with a few birds reaching Jutland and Great Britain (Fig. 2b). The colony De Beer is situated too far south to enable the birds to reach the northern Wadden Sea; most birds are found in the Netherlands and northern France (Fig. 2c). Birds from Farne Islands are found nearly exclusively on the British east coast, a few birds reaching the Netherlands (Fig. 2d).

Table 5: Dispersal from Sandwich Tern colonies. The percentage moving in the "wrong" direction indicates the proportion moving in the opposite direction to the migrational. Numbers in brackets refer to the number of recoveries from June—September.

Colony	Percentage moving in "wrong" direction	Percentage passing 1000 km limit	Dispersal rate (%)	
Treskelbakkeholm	30.8 (26)	21.4	23.4±4.4	
Hirsholmene	14.6 (41)	12.7	14.0±1.8	
Fjandø	36.8 (19)	25.0	18.8±3.4	
Trischen	31.8 (107)	13.3	16.3 ±1.4	
Scharhörn	50.0 (46)	18.1	15.5±1.7	
Griend	47.5 (59)	4.4	15.6±1.5	
De Beer	40.6 (32)	6.4	14.0±1.4	
Farne Islands	50.0 (54)	25.4	23.3±2.9	

No marked preference for dispersal in the opposite direction to the migrational direction exists (Table 5). Sandwich Terns moving in the "wrong" direction range from 15-50% in the months June-September. Dispersal rates range from 14.0-23.4% with large values for the two distant colonies, Treskelbakkeholm and Farne Islands, and Fjandø. The proportion of birds moving beyond the 1000 km boundary during the period June— September ranges from 4.4—25.4%, again with the highest values for Farne Islands, Fjandø and Treskelbakkeholm which are furthest away from the winter quarters. The agreement between the theoretical dispersal rates and the actual distribution of recoveries is close (Fig. 3). The best agreement is found for birds from Scharhörn, Griend and De Beer, while some deviation is found for Farne Islands birds and, to a smaller degree, for birds from Hirsholmene and Trischen. These indicate that in each case a smaller than expected proportion of the birds pass beyond a certain limit. This limit is situated 500 km away from Hirsholmene, 450 km away from Trischen and 250 km away from Farne Islands which may indicate the primary dispersal ranges of birds from these colonies. Differences in the dispersal distances in the months July, August and September are shown in Table 6. In July birds have already moved up to 620 km. The median distances of recovery range from 30 to 190 km. In August some Sandwich Terns have moved up to 2200 km with medians ranging from 46 to 265 km. The median distances of recovery seem not to follow any pattern, as birds from the northern colonies do not move any further than those from the southern colonies. In September more birds have started a real migration, some birds reaching the African winter quarters more than 5000 km away. Median distances range from 215 to 835 km with no marked distribution. The increase in median distance from August to September varies strongly. Birds from Fjandø have only covered 6% of the September distance in August, while Scharhörn birds have covered 95% of the September distance in August.

Dispersal rates and dispersal distances seem not to be influenced by the distances of the colonies from the winter quarters, although the most distant colonies have rather high dispersal rates. More of the birds from these colonies seem to start migrating before the end of September and 20—25% cover over 1000 km. This picture may be biased by differences in

Table 6: Dispersal distances from Sandwich Tern colonies. The values indicate distances in kilometers and the number of recoveries (N). A dash indicates a month with less than 6 recoveries.

Colony	July August				September				
	Range	Median	N	Range	Median	N	Range	Median	N
Treskelbakkeholm	32—370	190	12	36—2200	135	8	30—5250	615	15
Hirsholmene		_		24-1350	230	36	127—1630	620	29
Fjandø		_		5—2110	45	20	220-2070	835	12
Trischen		_		17—2165	135	81	20—2995	300	42
Scharhörn		_		<i>7</i> —940	265	49	50— 900	280	21
Griend	0-250	30	9	10—1040	190	60	20—4740	390	22
De Beer	10-620	150	15	20—760	230	37	30—1040	450	18
Farne Islands				10—560	125	42	10—4750	215	22

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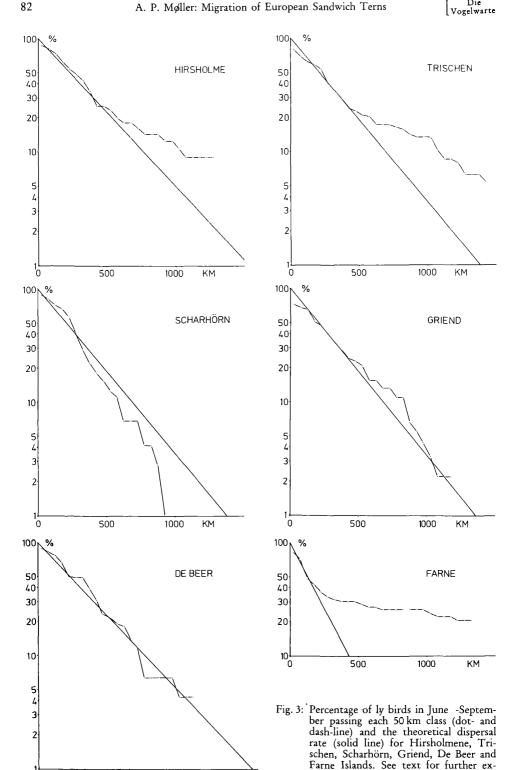


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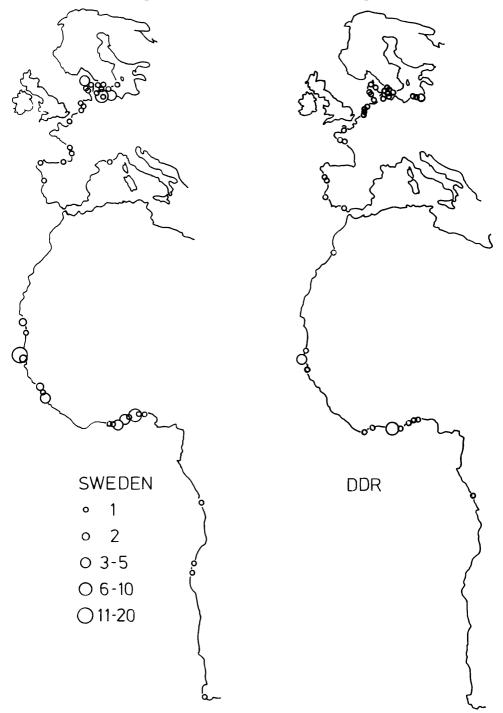


Fig. 4: Recoveries of birds from Sweden up to 1975 and GDR (DDR) up to 1976.

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Die Vogelwarte

geomorphology and hydrography of the neighbourhood of the colonies. Local differences in the occurrence and amount of fish present may furthermore influence the dispersal of the birds after the breeding season. The biological significance of dispersal seems to be for members of a colony to avoid food competition after the young fledge. When the birds have scattered over some hundred kilometres during this critical period, while the juveniles learn to catch fish (Dunn 1972), they are able to get enough food on their own or especially by feeding from their parents and at the same time be able to practise fishing. In a long-lived species such as the Sandwich Tern the survival of the young seems not to be as important as the survival of adult birds at their most productive age. Therefore, the avoidance of competition between juveniles and their parents and other adults seems to be particularly critical during the post-fledging period.

9.2. Post-breeding dispersal

Sandwich Terns change their colonies so often that there is little chance of detecting post-breeding dispersal of adult birds in the ringing recoveries. Indirect evidence from birds north of the breeding range suggests that such dispersal does occur. Post-fledging parental care is prolonged in the Sandwich Tern and lasts for at least several months, the young becoming independent during their first winter (DUNN 1972). Adults are therefore supposed to follow their own young on their dispersal. Birds with an unsuccessful breeding may have a dispersal period, too, although this remains only speculative. An increasing number of ringed adults in Denmark may help to elucidate some of these problems.

10. Migration

The range of the Sandwich Tern has been divided into four main areas with reference to migration: 1) Europe (the European continent), 2) West Africa (the northern part of Africa south to Liberia) 3) Guinea Gulf (Ivory Coast to Ghana) and 4) Southern Africa (Nigeria to South Africa).

10.1. Sweden

The Swedish population was established in 1911 (Sof 1978), probably by immigration from Denmark. The distribution of the 126 recoveries reported (Fig. 4) corresponds to that of the Danish birds, with most winter recoveries in West Africa, fewer recoveries in the Guinea Gulf and very few birds in Southern Africa. Dispersing birds seem to be concentrated in the Baltic and Danish waters with a few reaching Poland to the east. Migration takes place around Jutland and along the west European coasts to Africa.

10.2. Denmark

The migrational pattern of Danish ly birds is outlined in Fig. 5. The occurrence of birds in various months in Senegal, Ghana and Angola is shown in Fig. 6. The spatial distribution on the four main areas Europe, West Africa, Guinea Gulf and Southern Africa in various months is shown in Fig. 7. The migration pattern of Danish 2—3y and 4y birds is indicated in Fig. 5.

10.3. German DR (DDR)

A total of 64 recoveries were reported up to 1976.

The population has grown through immigration since 1957, especially from Danish, Swedish and West German colonies (Nehls 1969). Most recoveries in Africa are found in the Guinea Gulf, fewer from West Africa and only one from Southern Africa (Fig. 4). The migration takes place along the west European coasts to the winter quarters in Africa. The birds disperse in the western Baltic and the inner Danish waters with a few birds reaching Poland.

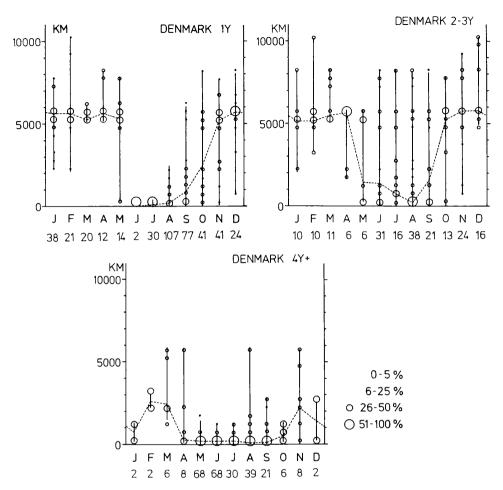


Fig. 5: Recoveries of Danish ly, 2—3y and 4y+ birds. The recoveries are distributed on 500 km classes. For each month the percentage of the total number of recoveries has been calculated for each 500 km class. Vertical lines connect the least and most distant recoveries. A dashed line connects the medians. Numbers refer to the numbers of recoveries in various months.

10.4 FR Germany

The spatial distribution of West German 1y birds is shown in Fig. 8. The temporal occurrence of West German recoveries in Senegal, Ghana and Angola is indicated in Fig. 6. The spatial distribution on the four main areas in various months is shown in Fig. 7.

The spatial distribution of West German 2-3y and 4y + birds is shown in Fig. 8.

10.5. Netherlands

The spatial distribution of Dutch ly birds is outlined in Fig. 9. The spatial distribution on the four main areas Europe, West Africa, Guinea Gulf and Southern Africa in various months is shown in Fig. 10.

The migrational pattern of Dutch 2—3y and 4y + birds is shown in Fig. 9.



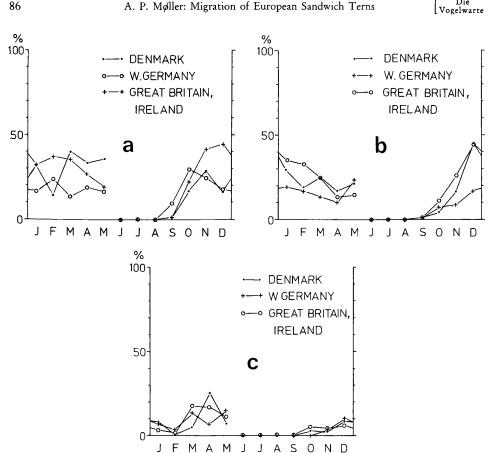


Fig. 6: Percentage of ly birds from Denmark, FR Germany, and Great Britain and Ireland in Senegal a, Ghana b, and Angola c, in different months.

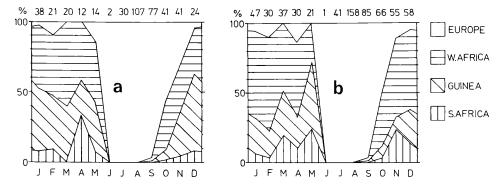


Fig. 7: Percentage of Danish (a) and West German (b) ly birds in Europe, West Africa, Guinea Gulf and Southern Africa in different months. Numbers at the top indicate the numbers of recoveries in the different months.

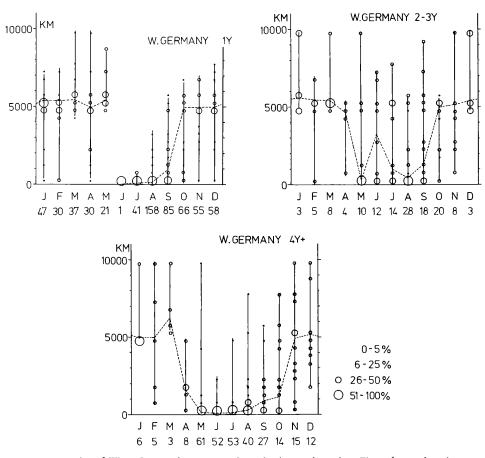


Fig. 8: Recoveries of West German ly, 2-3y and 4y+ birds. See legend to Fig. 5 for explanations.

10.6. Great Britain and Ireland

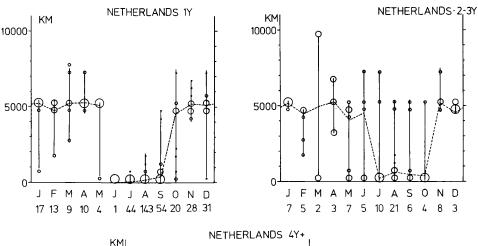
The spatial distribution of British and Irish ly birds is shown in Fig. 11. The temporal occurrence of British-Irish recoveries in Senegal, Ghana and Angola is indicated in Fig. 6. The distribution of recoveries in the four main areas is outlined in Fig. 10.

The spatial distribution of British and Irish 2—3y birds is shown in Fig. 11. The temporal occurrence of British-Irish recoveries in Senegal, Ghana and Angola is indicated in Fig. 12. The spatial distribution on the four main areas in various months is shown in Fig. 13.

The migrational pattern of British and Irish 4y + birds is outlined in Fig. 11. The temporal occurrence of British-Irish recoveries in Senegal, Ghana and Angola is indicated in Fig. 12. The spatial distribution on the four main areas Europe, West Africa, Guinea Gulf and Southern Africa is shown in Fig. 13.

10.7. Western France

A total of 157 recoveries were reported up to 1979. Most recoveries in Africa are from West Africa with many from the Guinea Gulf and only few from Southern Africa north to Natal (Fig. 14). The birds disperse in the Channel and the Bay of Biscay, a few birds reaching, Britain, Ireland and the Netherlands. Campredon (1978) has analysed the recoveries of birds ringed on Banc d'Arguin, Gironde.



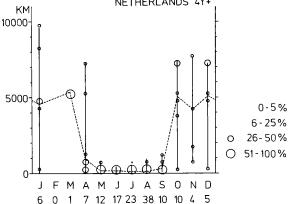


Fig. 9: Recoveries of Dutch ly, 2-3y and 4y+ birds. See legend to Fig. 5 for explanations.

10.8. Camargue

A total of 27 recoveries were reported up to 1979. Sandwich Terns first bred on the Camargue in 1953 (ISENMANN 1972). Two retraps of British Sandwich Terns indicate that at least some of the birds have immigrated from Britain. Most African recoveries are from the Guinea Gulf with few in West Africa and Southern Africa (Fig. 14). The birds disperse in the northern part of the western Mediterranean some birds reaching Italy in the east.

10.9. Black Sea

About 30.000 pairs of Sandwich Terns breed in the northern part of the Black Sea from Odessa to Krim (Borodulina 1966, Ardamatskaya 1977). A few colonies are found in the Danube Delta (Kiss 1978). The population is not genetically totally isolated as one bird has changed its breeding ground from Odessa to Denmark and another vice versa. Ardamatskaya (1977) has recently analysed the recoveries. Most of the birds stay within the Black Sea and the Mediterranean. Only 6% are recovered west of Gibraltar. In the Mediterranean 80% are recovered in the western part eastwards to Italy and Tunisia, while 14% are recovered in the eastern part. This distribution may reflect the fact, that the western part of the Mediterranean has the largest primary production and the highest salinity (Ashmole 1971). A single bird in Dakar, Senegal is highly diverging from the rest of the recoveries. It may be a bird originally of west European origin.

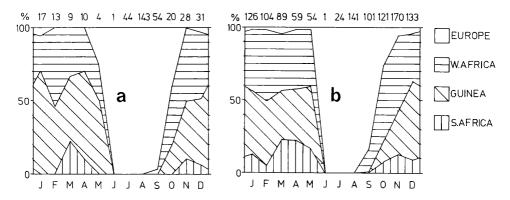


Fig. 10: Percentage of Dutch (a) and British and Irish (b) ly birds in Europe, West Africa, Guinea Gulf and Southern Africa in different months. See legend to Fig. 7 for further explanations.

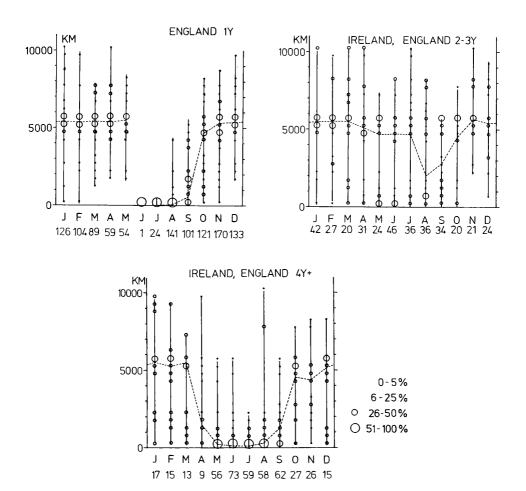


Fig. 11: Recoveries of British and Irish ly, 2-3y and 4y+ birds. See legend to Fig. 5 for explanations.

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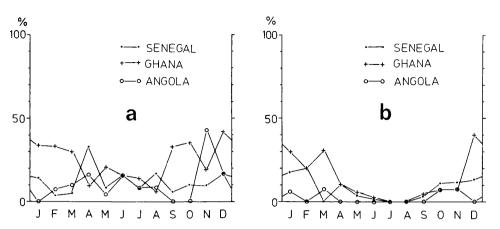


Fig. 12: Percentage of 2—3y (a) and 4y+ (b) birds from Great Britain and Ireland in Senegal, Ghana and Angola in different months.

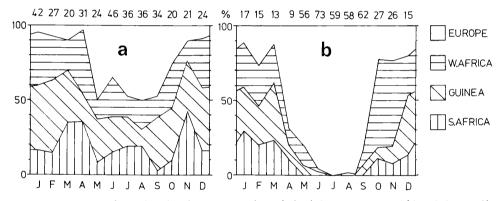


Fig. 13: Percentage of British and Irish 2—3y (a) and 4y+ (b) birds in Europe, West Africa, Guinea Gulf and Southern Africa in different months. See legend of Fig. 7 for further explanations.

10.10. Caspian Sea

The occurrence of Sandwich Terns on the Caspian Sea is sporadic and the birds are nomadic. There are about 20.000 pairs in this presumably totally genetically isolated population without contact in breeding or winter range with other populations (Poslavskii & Krivonosov 1976).

11. Comparative analysis of migration patterns

11.1. Comparison of the populations in Denmark, West Germany, Netherlands and Britain and Ireland

11.1.1. 1y birds

British and Irish and Dutch birds cover a rather short distance by August and especially September compared to Danish and especially West German birds (Fig. 5, 8, 9, 11). This slow movement may indicate a leap-frog migration (SALOMONSEN 1955), but the winter distribution of the populations does not support such a hypothesis. In October Danish birds are nearer to the breeding grounds compared to the other three populations. During the rest of the year ly

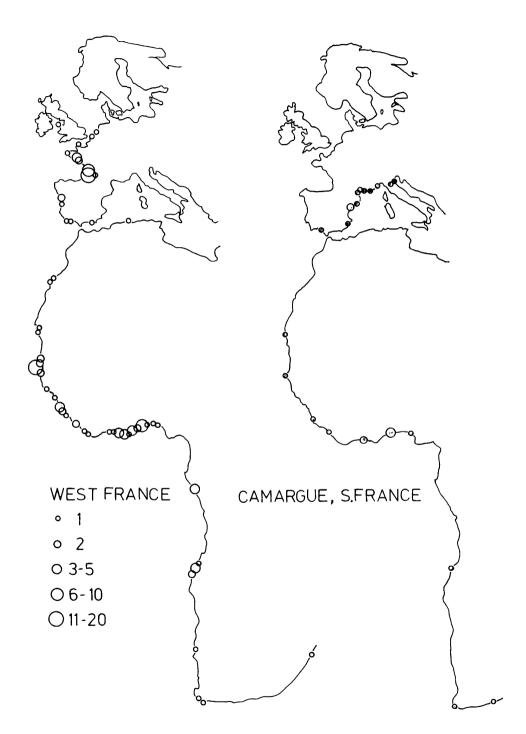


Fig. 14: Recoveries of birds from Western France up to 1979 and from Camargue, South France up to 1979.

birds from the four areas have an extremely similar distribution. Generally more British and Irish birds are found in Africa compared with those from other countries (71.9% v. 32.9—46.7% for the other countries). This is due to a much higher mortality in Europe among birds from the continental populations. More West German birds are recovered in West Africa (61.7%) compared to the other countries (46.2—48.1%), while in the Guinea Gulf the picture is in the opposite direction with much fewer recoveries from West Germany (23.8%) compared to the other countries (37.7—42.2%). The recoveries in Southern Africa amounts to 10.6—14.6% of the total number of African recoveries.

11.1.2. 2-3y birds

The northward return of some of the immature birds during summer shows differences between the countries of origin. Danish and West German birds return between May and September, while Dutch and British and Irish birds are later returning, in July to October (Figs. 5, 8, 9, 11). Furthermore, British and Irish Sandwich Terns are less likely to return to areas near the breeding grounds than the other populations in northern Europe. The recoveries of British and Irish birds in Europe make up a smaller part of the total number of recoveries (26.8%) compared with those from other countries (45.8—47.7%). The distribution of African recoveries shows a much smaller proportion of British and Irish birds in Western Africa (33.3%) compared with the other populations (43.5—51.1%), while more Dutch (31.2%) and especially British and Irish birds (41.3%) are found in the Guinea Gulf compared to Danish and West German birds (23.1 and 27.7%). Recoveries from Southern Africa comprise 17.8—33.4% with fewest Dutch and most Danish birds.

11.1.3. 4y + birds

Generally very few recoveries are available from Danish, West German and Dutch birds outside the breeding season. As for the two other age classes fewer British and Irish birds are recovered in Europe (72.8%), compared to the other populations (79.7—83.4%), although the difference is smaller than for the previous age classes (Figs. 5, 8, 9, 11). The African recoveries show few Dutch birds in West Africa (31.9%) compared to other populations (42.4—47.1%). Much more Danish birds are recovered in Guinea Gulf (42.4%) compared to ther other populations (19.9—29.4%). Recoveries in Southern Africa are dominated by Dutch recoveries (45.2%) compared to 15.3—33.9% for the other countries, but the differences may be due to coincidence, as the number of recoveries from Denmark and the Netherlands is small.

The Sandwich Tern population of Britain and Ireland seems partially to be isolated from the continental populations, although some affinities to the Dutch population seems to exist. The migration pattern of Danish, West German and to a lesser degree Dutch birds is similar.

11.2. Other western European populations

The distribution of Swedish and East German recoveries is very similar to the previously examined continental populations with many European recoveries (58.7 and 65.6%). Many birds are recovered in Guinea Gulf (40.4% for Sweden and 63.6% for GDR) and very few in Southern Africa (7.7% for Sweden and 4.5% for GDR) which is farthest away from the breeding grounds.

Many birds from western France are recovered in Africa (61.1%) compared to the other populations. Recoveries in Africa are dominated by West Africa with 56.3% of the recoveries and only very few birds in Guinea Gulf (27.1%). The French birds are therefore similar to the British ones in the proportion of the recoveries in Europe, while the distribution of recoveries in Africa is similar to the continental populations.

Recoveries from Camargue, South France are too few to be analysed.

12. Zoogeographical aspects of migration patterns

The western European populations are obviously totally synhiemic, and even Salomon-SEN (1955) used the Sandwich Tern to illustrate synhiemic populations. Analyses of the migration of the different populations in western Europe show that no leap-frog type of migration exists. The northern populations do not migrate further south compared to the other populations. On the other hand, the Black Sea population demonstrates leap-frog migration with the western European populations; the migration route is short with the winter quarters situated near the breeding grounds. The Black Sea population is partially synhiemic with the western European populations (MÜLLER 1959, LANGHAM 1971). Only 6% of recoveries from the Black Sea population occur west of Gibraltar, whilst western European birds occur in the Mediterranean infrequent (Table 7). Danish birds are found there most often, followed by British and Irish, West German and Dutch birds. For all four populations, juveniles (2—3y) occur much more frequently compared to the other age classes but ly birds are only rarely seen in the Mediterranean (Table 7). Anyhow, only 0.68% of the recoveries of all western European birds are from the Mediterranean and even fewer birds reach the Black Sea, a total of two or 0.05% (Tabel 7):

Table 7: Recoveries in the Mediterranean and the Black Sea. Percentage recovered from different countries in different age classes.

Recoveries in the Medit	erranean				
Country and age class		Recoveries	Total recoveries	Percentage	
Denmark	ly	0	427	0.0	
	2́—3y	6	144	4.1	
	4y+ ´	2	162	1.2	
	ly+	8	733	1.1	
West Germany	ly	0	628	0.0	
·	2—3y	5	195	2.6	
	4y+	1	380	0.3	
	ly+	6	1203	0.5	
Netherlands	ly	0	374	0.0	
	2—3y	0	86	0.0	
	4y+	1	133	0.8	
	ly+	1	593	0.2	
Great Britain, Ireland	ly	3	1103	0.3	
	2—3y	7	361	1.9	
	4y+	5	449	1.1	
	ly+	15	1913	0.8	
All countries	ly	3	2532	0.1	
	2—3y	18	786	2.3	
	4y+	9	1124	0.8	
	ly+	30	4442	0.68	
Recoveries in the Black	Sea				
All countries	ly+	2	4442	0.05	

Copenhagen 7007381 17. vi. 1967 Deget (57.28 N, 10.35 E), Denmark

/?/ oo.viii.1969 Odessa Bay (46.32 N, 30.48 E), Ukraine, USSR

London 42000038077 19.vii.1967 Farne Islands (55.38 N, 01.37 W), Great Britain

/?/ 21.vi.1974 Sfíntu Gheorghe (44.52 N, 29.36 E), Rumania

In addition one Soviet ringed bird has been retrapped on the breeding grounds in Denmark:

Moscow P319005 3.vii.1974 Asovskoje More (46.00 N, 36.30 E), Ukraine, USSR v 11.vi.1977 Agger Tange (56.47 N, 08.13 E), Denmark

The population of the Caspian Sea is totally allohiemic to both the western European populations and the populations of the Black Sea. This separation seems to be of very recent origin as no subspeciation has taken place. Heavy droughts in the Aralo-Caspian area in the

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latest centuries (Kalela 1946) may have cut off the connection between the Black Sea and the Caspian Sea populations. The winter quarters of the Caspian Sea population and the Black Sea/western European populations are totally separated, as the Caspian birds are only rarely seen further south than Sudan and more often occur along the coasts of Iran (Cave & Macdonald 1955, Dementiev & Gladkov 1969, Erard & Etchécopar 1970), while western European birds have been recovered north to St. Lucia, Zululand, South Africa. Hence, the chance of subspeciation in Sandwich Terns in the Caspian Sea seems to exist. North American birds of the subspecies acuflavida may accidentally reach Europe, as a single bird ringed in North Carolina, USA 23 June 1978 was recovered in the Netherlands 23 December 1978 (Scharringa 1979).

(To be continued).

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Zur Variabilität von Körpergewicht und Flügellänge des Grünlings (Carduelis chloris) in Berlin

Von Dieter Westphal

Einleitung

In verschiedenen Gegenden Mitteleuropas wurden in neuerer Zeit biometrische Untersuchungen an Grünlingen durchgeführt. PRILL (1975) veröffentlichte Flügelmeßwerte von im Winterhalbjahr bei Serrahn, DDR, gefangenen Grünlingen. Weitere Angaben über Flügellängen von Winterpopulationen liegen aus Südfinnland (LAAKSONEN et al. 1974) und der Schweiz (SUTTER 1946) vor. Eine besonders ausführliche biometrische Analyse unter Einbeziehung des Körpergewichts wurde von ROBERT (1977) bei überwinternden Grünlingen in Namur, Belgien, durchgeführt. Körpergewichte wurden außerdem in der Tschechoslowakei (MILES 1968) und in der DDR (PRILL 1974) bestimmt und deren Veränderungen im Jahresverlauf verfolgt.

Im Rahmen von populationsbiologischen Untersuchungen und Mauserstudien an Grünlingen konnten auch in Berlin Daten zu Körpergewicht und Flügellänge gesammelt werden. Die Ergebnisse dieser Messungen werden im folgenden dargelegt und mit den vorhandenen Literaturdaten verglichen.

Material und Methode

Vom Autor wurden in den Jahren 1972 bis 1979 in Berlin (West) Flügelmessungen an 538 und Körpergewichtsbestimmungen bei 517 zur Beringung gefangenen Grünlingen vorgenommen. Die Gewichte wurden mit einer Federwaage auf 0,5 g genau bestimmt. Die Wägungen erfolgten über den Tag verteilt, so daß die Gewichtsangaben als Tagesdurchschnittswerte angesehen werden können. Die Flügellänge (jeweils des linken Flügels) wurde nach der Methode "Kleinschmidt" (Kelm 1970), d. h. maximale Streckung des Flügels durch Andrücken an das Anschlaglineal mit einer Genauigkeit von 0,5 mm ermittelt.

Geschlechtsbestimmung

Die Geschlechtsbestimmung bereitet im allgemeinen keine Schwierigkeiten und kann zu allen Jahreszeiten und mit großer Sicherheit auch schon bei nur wenige Wochen alten Jungvögeln durchgeführt werden (vgl. Drost 1931, Svensson 1970). Wichtigstes Unterscheidungsmerkmal ist die Gelbfärbung der Handschwingen sowie der drei äußeren Schwanzfedern, wo das Gelb beim 3 fast die gesamte Breite der Außenfahnen einnimmt und beim $\mathbb Q$ nur einen schmalen Streifen am äußeren Saum bildet.

Altersbestimmung

Entsprechend den Richtlinien der Vogelwarten in der Bundesrepublik wird in dieser Untersuchung differenziert zwischen diesjährigen (d) bzw. vorjährigen (v) und nicht diesjährigen (nd) bzw. nicht

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