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Time of breeding, causes of recovery and survival of European Sandwich Terns *(Sterna sandvicensis)*

By Anders Pape Møller

1. Introduction

The vast number of ringing recoveries accumulating annually calls for new methods to evaluate their usefulness in survival calculations and etimates of mortality factors. When temporal changes are dicuscced, even further caution is needed due to the large number of variables being involved.

In the present paper an analysis of breeding season, mortality factors and survival rates of the Sandwich Tern will be presented.

2. Materials and methods

Recoveries from the European countries have been used as described by Møller (1981—1982). Sandwich Terns reported dead of unknown causes have been excluded from the section on causes of recovery, as they comprised less than 5 % of the total number of recoveries. Three age classes have been considered here, viz. juveniles (from ringing until May 31 the year following ringing, 1y), immatures (from June 1 the year following ringing to May 31 three years following ringing, 2—3y) and adults (from June 1 three years following ringing, 4y+).

For the spatial distribution sections, 5 areas have been considered, viz. 1. N Europe (southwest to Great Britain and the Netherlands), 2. W Europe (Belgium to Spain, Portugal and the European part of the Mediterranean), 3. W Africa (African continent from Tunisia to Liberia), 4. Gulf of Guinea (Ivory Coast to Ghana), and 5. S Africa (Nigeria to South African Republic).

Ring wear: Rings from birds of known age have been supplied from Denmark, the Netherlands and the British Isles. Rings have been weighted on a Mettler weight to the nearest mg.

Breeding season: Ringing dates have been taken as an indication of the breeding season. For Danish birds only, a comparison of all birds ringed (with Zoological Museum rings) and those recovered has been possible.

Causes of recovery: Causes of death according to the recoveries are examined. Three categories have generally been used, viz. bird shot, trapped and 'found dead'.

Survival rates: Survival has been calculated in a number of ways for various age classes. Pre-fledging mortality has been analysed from recoveries at the ringing site before fledging ('loco' recoveries, from Latin *locus* — place, site). 1y mortality has been calculated as the number of 1y recoveries per 1 000 pulli ringed.

Methods for calculating mortality in adult birds have been discussed in recent years (e. g. Seber 1971, Cavé 1977, North 1978). From the thorough analyses made by North (1978) on various methods to calculate mortality, Lack's (1951) method seems te be the most appropriate one. Seber's (1971) age specific survival rates have a number of preconditions to be fulfilled before usage. Several of these are not fulfilled by the data to be analysed in this paper: 1) The annual probability of a recovery being reported has to be equal for all birds and all calendar years. 2) The annual reporting probability may depend on the age of the bird, but not on the calendar year. Furthermore, only short time sequences (4 year periods) can be analysed together making a large number of ringed birds and recoveries necessary to avoid out of range (above 1.0) estimates of survival. Different modifications suggested by North (1978) (using different parameter constraints, pooling some of the data using the EM algorithm with boundary constraints) have resulted in out of range estimates of mortality rates in a fraction of the cases.

Lack's (1951) method, giving a constant survival rate, may be applied to adult birds only. Computer simulations give good estimates using this method on as few as 20 recoveries (North 1978). Only estimates based on 20 or more recoveries have been calculated in this paper. Juvenile survival rates have to be estimated separately.

The survival rate of a specific age class is

$$\hat{s}_i = \frac{N_{i+1}}{N_i}$$

where $N_i = \sum_{p=i}^{t_i} d_p$ and d_p are the recoveries at age p. The standard error of $\hat{s}_i$ is

$$\text{s. e. } (\hat{s}_i) = \frac{1}{N_i} \left(\frac{d_i \cdot N_{i+1}}{N_i} \right)^{1/2}$$

The adult survival rate ($\hat{s}$) is calculated as

$$\hat{s} = \frac{\sum_{i=4}^{t} (i-4) \cdot d_i}{(N - d_1 - d_2 - d_3) + \sum_{i=4}^{t} (i-4) \cdot d_i}$$

using the symbols mentioned above. The standard error of this survival estimate has been calculated as

$$\text{s.e. } (\hat{s}) = (1-\hat{s}) \left(\frac{\hat{s}}{N - d_1 - d_2 - d_3} \right)^{1/2}$$

Separate calculations of survival rates in relation to the recovery cause have been made.

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3. Breeding season

3.1. Results

The breeding season according to ringing dates of Sandwich Terns later recovered is shown for the N European population in Fig. 1. A retardation can be seen from northeast to southwest. The Dutch population deviates from the usual normal distribution with a smaller peak in early June and a major one around June-July. Several factors may be responsible for this pattern. One possible cause is different food conditions in the Wadden Sea area and in S Holland. Among young ringed in the Wadden Sea 33.9 % (N = 289) were ringed before June 24, while 33.5 % (N = 272) of those ringed in the Netherlands outside the Wadden Sea area were ringed before that date. The two peaks in breeding activity may be due to different populations. This can be caused by immigration following the pollution accident in the 1960's when a large fraction of the Dutch population died (KOEMAN et al. 1967). Immigration of northern birds from Germany and Denmark to the Netherlands may have caused an early peak in the breeding season. Several Danish and German Sandwich Terns have in fact been reported breeding in the Netherlands following the population decrease in the 1960's. If immigration is the cause,

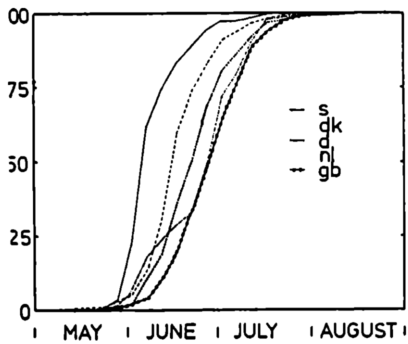

Fig. 1: Cumulative distribution of ringing dates for Sandwich Tern pulli. s — Sweden (N = 125), dk — Denmark (N = 640), d — Germany (N = 968), nl — Netherlands (N = 589), gb — British Isles (N = 2292). 5 days periods.

then the early peak should not be present before 1960. In fact, more birds have been ringed during the period May 21 to June 14 after 1959 compared to the situation for the years 1910—1959 (1910—1959: 38 ringed before June 15, 194 ringed after June 14, 1960—1975: 104 ringed before June 15, 253 ringed after June 14, $\varkappa^2_{(1)} = 11.8$, $p < 0.001$).

The median ringing date is displaced from June 5 in Sweden to june 27 in the Netherlands and the British Isles (Table 1). Similarly, the main breeding period covering 10—90 % of all ringing increased in length from north to south with a minimum of 25 days in Sweden and a maximum of 39 days in the Netherlands (Table 1). The length of the total ringing period was largest in Denmark (84 days) and Germany (86 days) with a shorter span south and especially north of this area (Table 1).

Table 1: Breeding schedule of European Sandwich Tern populations based on ringing data.

	Sweden	Denmark	Germany	Netherlands	British Isles
First pullus ringed	26 May	16 May	16 May	23 May	28 May
Last pullus ringed	19 July	8 August	10 August	7 August	6 August
Breeding period (days)	54	84	86	76	70
Median ringing date	5 June	15 June	21 June	27 June	27 June
Main ringing period 10—90 % of ringing (days)	25	28	35	39	32

3.2. Discussion

The breeding season of Sandwich Terns may be described from the ringing dates of birds recovered. To get a precise description of the breeding season, young have to be ringed at a certain rate throughout the breeding season at a certain age. No possibility exists to check these preconditions which here are supposed to be fulfilled.

Contrary to the normal retardation of breeding seasons from south to north (e. g. Lack 1954), an opposite trend was found in the Sandwich Tern. This may be caused by different non-temperature related trends in oceanographical conditions influencing the food supply first to adult Sandwich Terns and later to pulli. Similarly, the main breeding period may be modified by food supply, the longest period being found in southern waters. The period of warmth of the spring used by fish for breeding may be of restricted length in northern latitudes compared to southern ones. A similar trend in breeding season has been found in the Herring Gull *Larus argentatus* populations in Danish waters: a gradient with a retardation of breeding when moving from the Baltic through the inner waters to the North Sea (Møller 1981).

The distribution of ringing dates of later recovered Sandwich Terns was approximate normal for all populations except the Dutch one. The two peaks in breeding activity were apparently not caused by differences in time of breeding within the Netherlands. However, a marked difference was found between the periods 1910—59 and 1960—75 with many early breeding terns in the latter period. This temporal shift in breeding time may be due to immigration of northern birds following the population decrease in the 1960's due to pollution. Several German and Danish birds have been recorded as breeding in the Netherlands during this period. It cannot be excluded that the change in breeding time is due to alterations in food occurrence. If this is so, food has only changed on a local scale as no comparable shifts in breeding time were found among the other populations.

4. Ring wear

4.1. Results

To have a check of ring wear and thereby a check of the applicability of recoveries for mortality calculations, rings used for different periods have been weighed. The age-weight relationship has been determined for Danish, Dutch and British Isles rings (Figs. 2—4), whereas German rings could not be obtained. A steady decrease can be seen during the first 10 years of use in weight of Danish and Dutch rings. Danish and Dutch rings had very similar age distributions, whereas the oldest British Isles rings were ca. 5 years old. However, the decrease in weight with age was statistically significant for all three ring samples (Danish rings: $r = -0.629$, $t_{(37)} = 4.92$, $p < 0.001$; Dutch rings: $r = -0.637$, $t_{(36)} = 4.96$, $p < 0.001$; British Isles rings: $r = -0.446$, $t_{(36)} = 2.99$, $p < 0.01$). The slopes for Danish and Dutch rings were very similar, but differed from the British Isles slope. However, this may be due to the different age distributions.

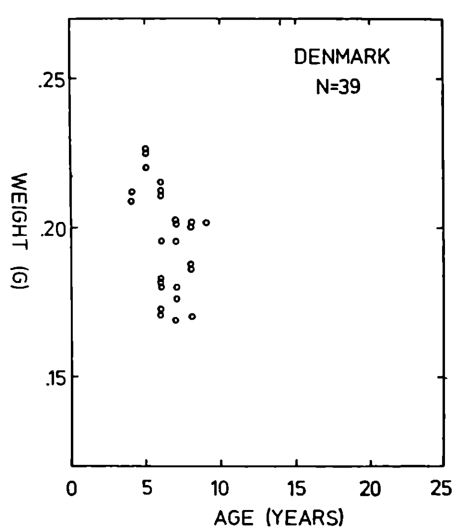

Fig. 2: Ring wear in Danish rings (Zoological Museum). Weight plotted against age.

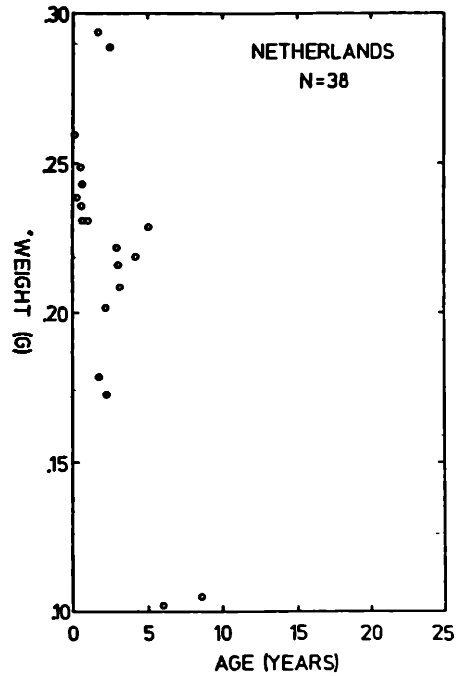

Fig. 3: Ring wear in Dutch rings (Vogeltrekstation Arnhem). Weight plotted against age.

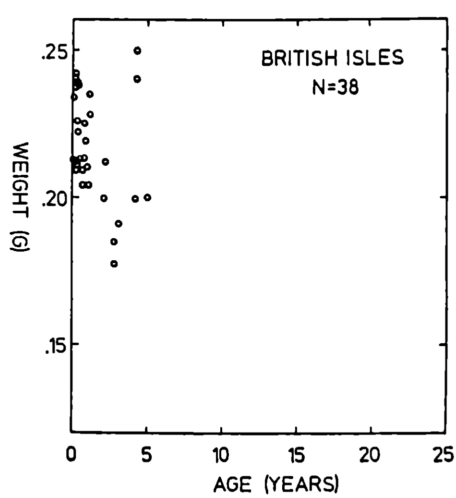

Fig. 4: Ring wear in British Isles rings (British Museum). Weight plotted against age.

4.2. Discussion

Ring wear may be quantified by loss of weight. However, legibility of rings may be even more important as light rings may be reported if they are legible. The legibility of specific rings has been good in all Danish rings, whereas two Dutch rings aged 7 and 10 years were both legible with difficulty. They were furthermore light and might have fallen off within a few years, if the birds had not died earlier. All British rings sampled were legible.

More severe ring wear has been seen in several other (especially oceanic) seabirds (e. g. COULSON & WHITE 1955, HARRIS 1980).

In conclusion, it can be said that a few rings aged 10 years or older may fall off or may not be returned to the ringing station when obtained due to illegibility.

5. Causes of recovery

5.1. Results

Variation in causes of recovery may occur due to the effects of population differences, age class differences, monthly differences, temporal changes and differences between migration and winter distribution.

Marked population differences in recovery cause exist (Table 2). Danish Sandwich Terns are shot more often than those from any other population. Shooting is common in Denmark and France. Dutch and German birds reach France in large numbers in early autumn, and shooting is a common cause of recovery for Sandwich Terns from these countries, too. British Isles birds are trapped more often than others and especially the ly and 2—3y age classes.

As various age classes spend their time in different areas differences in cause of recovery are expected. Immature Sandwich Terns spend their time in the winterquarters and trapping is more in this age class than in the others (Table 2). Shooting is more common in the 2—3y age class compared to juveniles and adults. Monthly variation in cause of recovery follows the distribution of the Sandwich Terns (Figs. 5—7). Strong increases in trapping frequency are seen during autumn as the terns reach the winter

Table 2: Causes of recovery (%) in different age groups of European Sandwich Tern populations.

Cause of recovery	Age 1Y	2—3Y	4Y+
Denmark			
shot	30.5	37.1	25.5
trapped	17.2	25.9	14.0
found dead	48.6	34.5	59.9
others	1.3	2.6	0.6
No. of recoveries	436	116	157
Germany			
shot	10.7	18.6	13.7
trapped	26.2	32.2	35.2
found dead	58.4	45.8	49.4
others	3.3	3.4	1.6
No. of recoveries	826	177	364
Netherlands			
shot	16.2	20.3	15.1
trapped	25.6	35.4	20.2
found dead	55.9	38.0	64.7
others	2.3	6.4	0.0
No. of recoveries	351	79	119
British Isles			
shot	4.5	7.3	7.3
trapped	49.2	53.7	33.4
found dead	34.6	25.9	48.6
others	11.7	13.1	6.9
No. of recoveries	1087	328	440

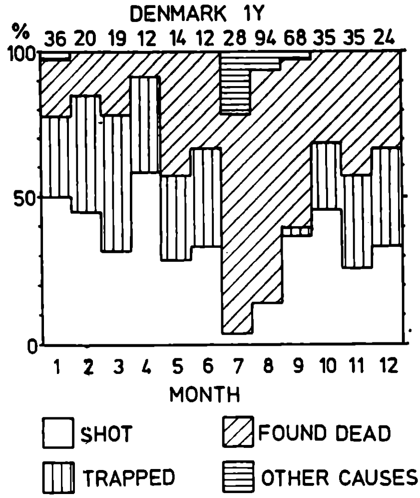

Fig. 5: Monthly distribution of recovery causes in Danish ly Sandwich Terns. Numbers at the top indicate numbers of recoveries.

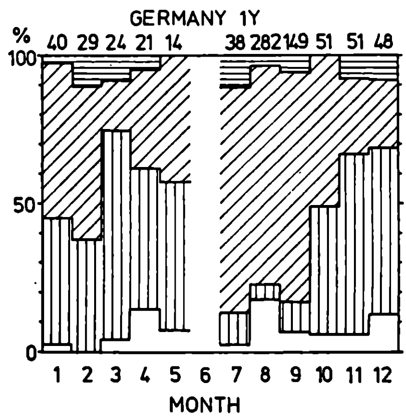

Fig. 6: Monthly distribution of recovery causes in German ly Sandwich Terns. Numbers at the top indicate numbers of recoveries. For explanations, see Fig. 5.

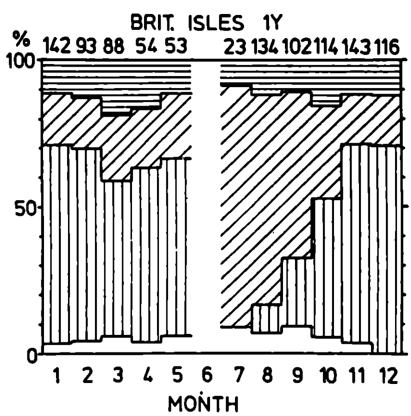

Fig. 7: Monthly distribution of redovery causes in British Isles ly Sandwich Terns. Numbers at the top indicate numbers of recoveries. For explanations, see Fig. 5.

quarters, and birds 'found dead' decrease synchronously. Large scale ringing since the beginning of the present century allows evaluation of temporal changes in cause of recovery (Table 3). Recovery due to shooting has decreased in importance in all age classes and areas, although the Danish decline in shooting frequency is far less compared to the other countries. Intensional trapping and birds 'found dead' comprise a larger fraction of the recoveries in the period 1960—1975 compared with 1910—1959.

Table 3: Temporal changes in causes of recovery (%) of European Sandwich Terns.

Cause of recovery	Age					
	1Y		2—3Y		4Y+	
	1910—59	1960—75	1910—59	1960—75	1910—59	1960—75
Denmark						
shot	41.5	25.2	42.0	33.3	48.6	18.9
trapped	14.8	18.4	28.0	24.2	5.7	16.4
found dead	35.9	54.8	30.0	37.9	45.7	63.9
others	0.7	1.7	0.0	4.5	0.0	0.8
No. of recoveries	142	294	50	66	35	122
Germany						
shot	19.6	6.2	50.9	4.8	37.8	7.6
trapped	20.3	29.1	22.6	36.3	18.9	39.3
found dead	55.7	59.1	22.6	55.7	43.2	51.0
others	4.3	5.5	3.8	3.2	0.0	2.0
No. of recoveries	276	550	53	124	74	290
Netherlands						
shot	44.3	2.5	46.4	5.9	35.6	2.7
trapped	13.0	31.8	21.4	43.1	13.3	24.3
found dead	41.7	62.7	32.1	41.2	51.1	73.0
others	0.9	2.9	0.0	9.8	0.0	0.0
No. of recoveries	115	236	28	51	45	74
British Isles						
shot	12.2	2.1	12.0	5.3	16.5	6.2
trapped	43.5	51.1	49.0	55.7	27.8	36.0
found dead	30.9	35.8	20.0	28.5	40.5	51.4
others	13.3	10.9	19.0	10.4	9.6	6.6
No. of recoveries	262	825	100	228	74	356

The distribution of birds affect their mortality agents (Table 4). Shooting is a common cause of death in W Europe, whereas trapping is widespread in the African winter quarters and especially so in W Africa and the Gulf of Guinea. Most N European recoveries of Sandwich Terns are reported as 'found dead'.

5.2. Discussion

The relative frequency of different causes of death as recorded by recoveries is probably highly biased. Sandwich Terns have different reporting probabilities according to their cause of recovery. Birds shot, for instance, are more often recovered than those killed by avian predators. However, a comparison of different populations and birds from different periods may reveal some of the variables affecting the relative frequencies of different mortality agents.

As the Sandwich Terns from various countries migrate through different areas and partly winter in different places (Møller 1981—1982), differences are expected to be found in the causes of death reported for the various populations. Birds from the British Isles aged ly and 2—3y are trapped for eating far more often than those from the other

Table 4: Causes of recovery (%) among Sandwich Terns in various areas.

Cause of recovery	Area				
	N-Europe	W-Europe	W-Africa	Guinea Gulf	S-Africa
Denmark					
shot	17.2	43.1	43.1	44.7	40.5
trapped	7.8	17.6	32.1	30.1	38.1
found dead	75.0	39.2	24.8	25.2	21.4
No. of recoveries	308	102	109	103	42
Germany					
shot	12.4	33.3	8.5	4.9	1.4
trapped	19.8	16.0	57.4	70.7	46.5
found dead	67.7	50.6	34.1	24.4	52.1
No. of recoveries	731	162	223	123	71
Netherlands					
shot	5.5	53.7	6.6	7.3	0.0
trapped	9.1	6.5	67.2	74.4	57.1
found dead	85.4	39.8	26.2	18.3	42.9
No. of recoveries	254	123	61	82	21
British Isles					
shot	4.4	17.2	5.4	3.9	9.0
trapped	17.7	34.9	67.1	81.8	55.7
found dead	77.9	47.9	27.4	14.3	35.2
No. of recoveries	453	215	423	433	122

European countries, probably because they winter in areas with heavy human persecution (Allison 1959, Dunn 1981). Furthermore, British Isles birds migrate to the African winter quarters very quickly in autumn compared to the other populations (Møller 1981—1982). Therefore, British Isles Sandwich Terns are exposed to trapping for longer time than other populations, and the terns furthermore escape common mortality agents in Europe due to a quick autumn migration.

The general increase in the importance of trapping Sandwich Terns may be an artefact. The increasing educational level in the African countries during the present century may have caused an increasing reporting probability of ringed birds. Following the independence of European colonies reporting probabilities may have decreased due to less efficient administration and mail services. The total picture remains obscure, probably with a slightly increasing recovery rate. In certain instances, such as Danish and German adult Sandwich Terns and Dutch juvenile and immature birds, the fraction of those reported trapped has more than doubled. An increase of that size may be due to a real increase in trapping activities. In British Isles birds, where trapping is the most important recovery cause in juvenile and immature Sandwich Terns, the increase is small.

6. Survival rates

6.1. Results

During their life birds are affected by different survival rates due to various mortality agents acting on them. Mortality risks may change with geographical location and the activities of the birds.

During the pre-fledging period mortality due to predation, starvation or other causes may reduce numbers significantly. British Isles and Danish Sandwich Terns have been reported dead on the breeding grounds before fledging, whereas comparable figures could not be obtained from Germany and the Netherlands (Table 5). Between 10 and 15 % of all recoveries originate from the place of ringing, but these mortality esti-

Table 5: Pre-fledging and post-fledging recoveries of Sandwich Terns.

Area	Pre-fledging recoveries (%)	Post-fledging recoveries (%)	No. of recoveries
Denmark	14.4	85.6	732
British Isles	11.7	88.2	2560

mates cannot be expected to represent absolute numbers due to differing reporting rates at the colony and elsewhere.

Breeding success can be estimated using recovery and ringing data (Fig. 8). If birds ringed during the different parts of the breeding season survive equally well the cumulative distribution of ringing dates for all birds and for recoveries should be similar. However, more birds are reported later on among those ringed early in the breeding season and especially so among those ringed in July. The differences are statistically significant (Kolmogorov-Smirnov test, D = 5.5 %, $p < 0.05$).

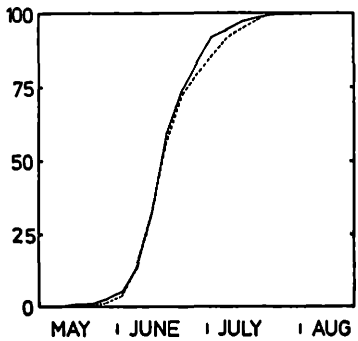

Fig. 8: Cumulative distribution of Danish Sandwich Tern ringing dates (broken line, N = 29462, Zoological Museum only) and ringing dates for recoveries (solid line, N = 640). 5 days periods.

Temporal differences in the distribution of pre-fledging mortality can be recorded by a comparison of ringing dates of 'loco' recoveries with ringing dates of birds recovered elsewhere (Figs. 9—10). Colony recoveries dominate among Danish Sandwich Terns late in the breeding season during July and among British Isles birds in May and early June. The differences are statistically significant (Kolmogorov-Smirnov test, D (Danish) = 20.9 %, $p < 0.005$, D (British Isles) = 13.5 %, $p < 0.001$).

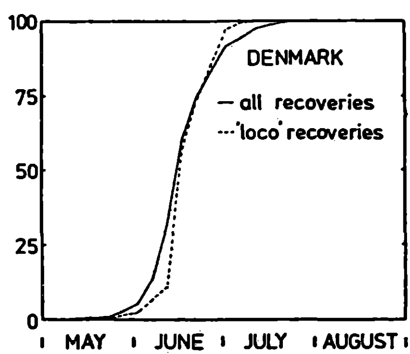

Fig. 9: Cumulative distribution of Danish Sandwich Tern ringing dates for 'loco' recoveries (N = 92) and all recoveries (N = 640). 5 days periods.

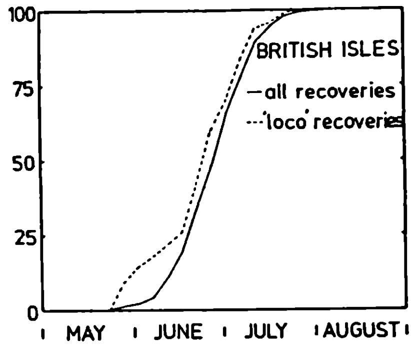

Fig. 10: Cumulative distribution of British Isles Sandwich Tern ringing dates for loco' recoveries (N = 268) and all recoveries (N = 2292). 5 days periods.

Future survival of Sandwich Tern young can be indicated by comparisons of ringing date distributions of birds of different age. A summary is given in Table 6, whereas computations have been made on cumulative five-days period distributions. 'Loco' recovery distributions deviated from those of all other age classes both among Danish and British Isles terns (Denmark: 'loco'-1y: D = 23.5 %, $p < 0.001$; 'loco' – 2 – 3y: D = 27.3 %, $p < 0.005$; 'loco' – 4y +: D = 25.5 %, $p < 0.005$. British Isles: 'loco' – 1y: D = 14.8 %, $p < 0,001$; 'loco' – 2 – 3y: D = 14.5 %, $p < 0.005$; 'loco' – 4y+: D = 16.6 %, $p < 0,001$, all Kolmogorov-Smirnov tests). However, the distributions of all other age classes were very similar except for British Isles 1y and 4y+ terns, which diviated significantly from each other (Kolmogorov-Smirnov test, D = 11.1 %, $p < 0.001$). Adult Sandwich Terns were to a larger extent ringed late in the breeding season compared with 1y birds recovered outside the colony area.

Table 6: Monthly distribution of ringing dates of recoveries of Sandwich Terns and of ringing dates of the Zoological Museum, Denmark.

Area and age group	Month				No. of recoveries
	May	June	July	August	
Denmark					
1Y 'loco'	1.1	83.7	15.3		92
1Y elsewhere	3.4	78.0	18.3	0.3	327
2—3Y	3.5	80.9	17.9		86
4Y+	1.5	84.4	14.1		135
Ringing	1.3	78.5	20.1	0.1	29460
Germany					
1Y elsewhere	0.4	68.6	30.7	0.2	560
2—3Y	1.6	69.0	28.9	0.8	129
4Y+	1.5	84.4	14.1		299
Netherlands					
1Y elsewhere	1.5	50.3	47.2	0.9	337
2—3Y	1.2	54.0	44.7		85
4Y+	0.8	43.7	54.9	0.8	133
British Isles					
1Y 'loco'	9.0	50.7	39.6	0.8	286
1Y elsewhere	0.3	49.1	49.7	0.8	1141
2—3Y	0.3	44.1	54.6	1.1	363
4Y+		41.6	57.5	1.0	520

Table 7: Age distribution of recoveries of Sandwich Terns.

Area	Age			No. of recoveries
	IY (%)	2-3Y	4Y +	
Denmark	67.0	20.2	12.8	640
Germany	63.8	19.6	16.6	986
Netherlands	63.7	13.9	22.4	589
British Isles	49.0	15.8	35.2	2292

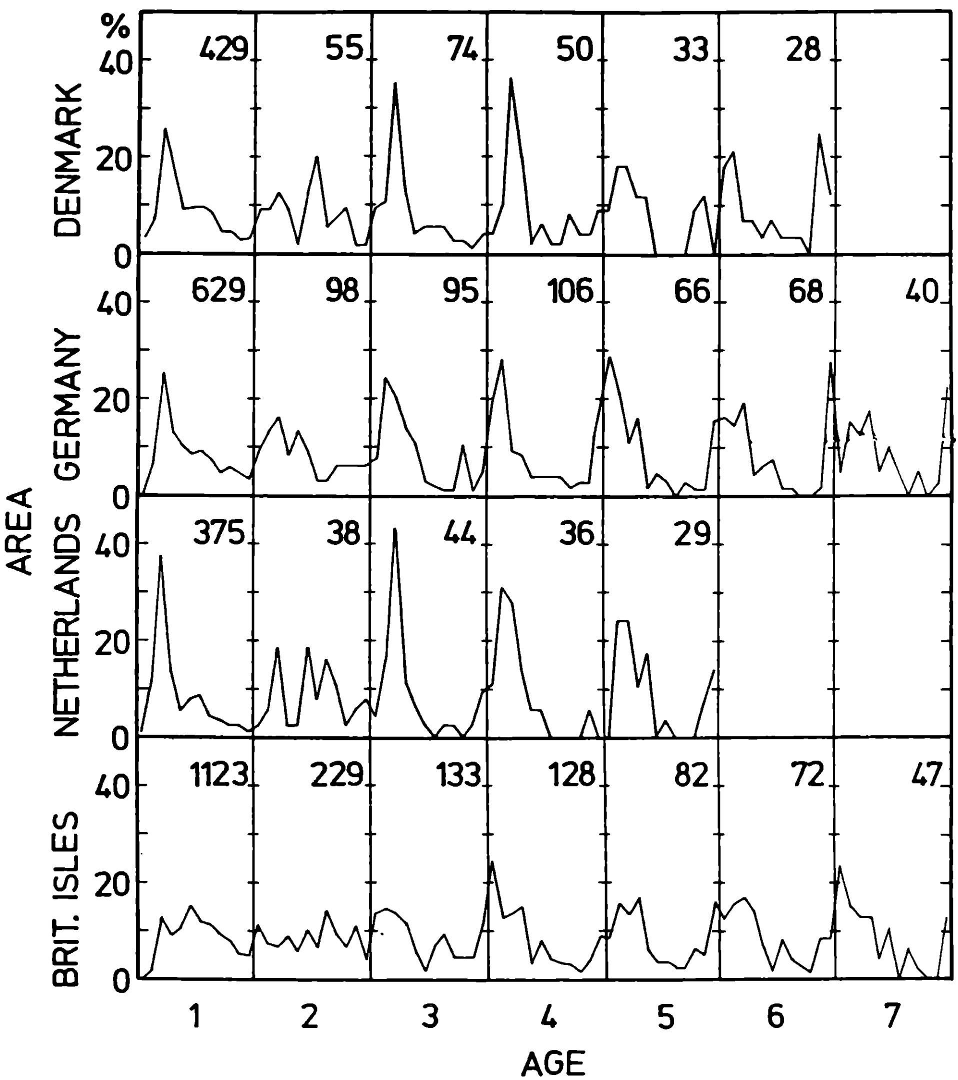

Fig. 11: Relative monthly distribution of Sandwich Tern recoveries from June to July within each year during the first seven years of life. In years with less than 20 recoveries, no calculations have been made. Numbers indicate numbers of recoveries in single years of life.

Juvenile survival differed strongly between various populations (Table 7). British Isles Sandwich Terns were recovered less frequently at an age of 1y compared to the other populations which had similar distributions of recoveries between the age classes. Temporal distributions of recoveries of differently aged birds are very similar for the continental populations, whereas British Isles Sandwich Terns show a marked peak in recovery during mid-winter among 1y terns contrary to the autumn peak recorded for other populations (Fig. 11).

Table 8: Adult survival estimates for Sandwich Terns of different ages based on recovery data. s_i = survival estimate of the i'th age class. Estimate ± standard error. Numbers in brackets indicate numbers of recoveries. If less than 20 recoveries are available, no estimate has been calculated. Recoveries from 1910—1964.

	Area			
Survival estimate	Denmark	Germany	Netherlands	Bitish Isles
$\hat{s}_1$	.554 ± .026 (359)	.392 ± .016 (974)	.420 ± .026 (362)	.492 ± .017 (901)
$\hat{s}_2$	.839 ± .026 (199)	.822 ± .020 (382)	.750 ± .035 (152)	.758 ± .020 (443)
$\hat{s}_3$	.647 ± .037 (167)	.828 ± .021 (314)	.719 ± .042 (114)	.824 ± .021 (336)
	.778 ± .040 (108)	.735 ± .027 (260)	.744 ± .048 (82)	.765 ± .025 (277)
$\hat{s}_5$	.714 ± .049 (84)	.707 ± .033 (191)	.721 ± .057 (61)	.745 ± .030 (212)
$\hat{s}_6$	.767 ± .055 (60)	.674 ± .040 (135)	.795 ± .061 (44)	.722 ± .036 (158)
	.739 ± .065 (46)	.670 ± .049 (91)	.743 ± .074 (35)	.789 ±.038 (114)
$\hat{s}_8$	.765 ± .073 (34)	.557 ± .064 (61)	.692 ± .091 (26)	.589 ± .052 (90)
$\hat{s}_9$	.769 ± .083 (26)	.735 ± .076 (34)		.717 ± .062 (53)
$\hat{s}_{10}$	.800 ± .189 (20)	.760 ± .085 (25)		.711 ± .074 (38)
$\hat{s}_{11}$				.741 ± .084 (27)
$\hat{s}_{12}$				.700 ± .102 (20)
Adult survival ($\hat{s}_{4+}$)	.748 ± .021 (108)	.697 ± .016 (260)	.734 ± .025 (82)	.727 ± .014 (277)

Juvenile survival estimates ranged from 0.39 to 0.55 with maximum in Denmark and minimum in Germany (Table 8), but estimates may be highly biased without compensation for differences in cause of recovery. Recovery rates for juvenile Sandwich Terns may be calculated as the number of recoveries per ringing effort (Fig. 12). There are indications of an increasing reporting rate. For Danish birds rates above 12 recoveries per 1000 pulli ringed have been found in 8 years and below 12 recoveries in 18 years before 1960, while 11 years during the period 1960—1975 had rates above and 4 years had rates below 12 recoveries ($\chi^2_{(1)} = 6.9$, $p < 0.01$). For British Isles Sandwich Terns the recovery rate was above 5 recoveries per 1000 pulli ringed in 7 years and below in 12 years for the period before 1960, whereas it was above in 8 years and below in 7 years for the period 1960—1975 ($\chi^2_{(1)} = 0.9$, n. s.).

Among immature Sandwich Terns a shift in distribution is seen between 2y and 3y birds leading to a peak autumn occurrence in European waters for 3y birds (Fig. 11).

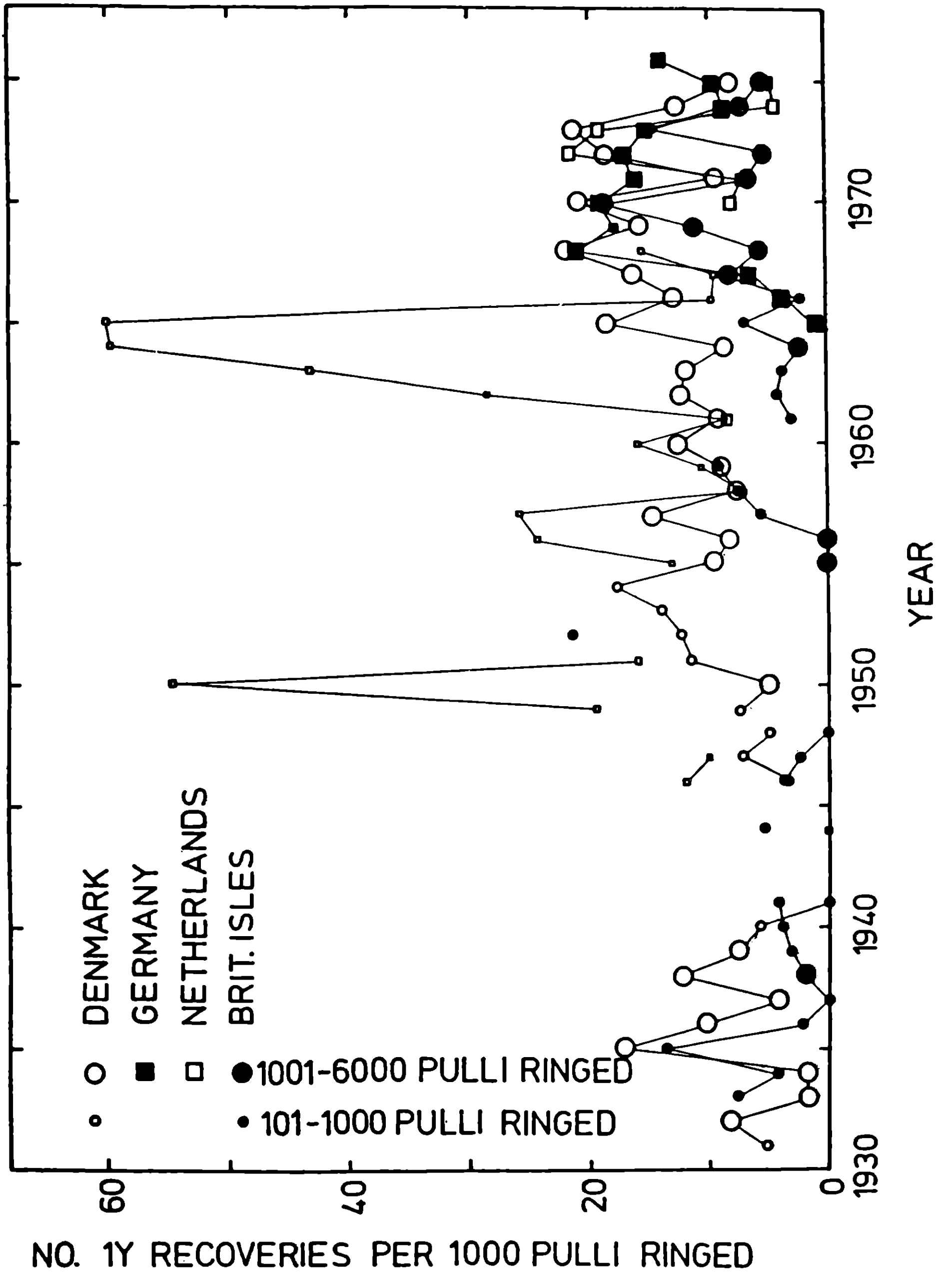

Fig. 12: Annual recovery indices calculated as number of first year recoveries per 1000 pulli ringed. No calculations have been made in years with less than 100 pulli ringed. Separate years ringing data have not been obtained from Germany for the period prior to 1965.

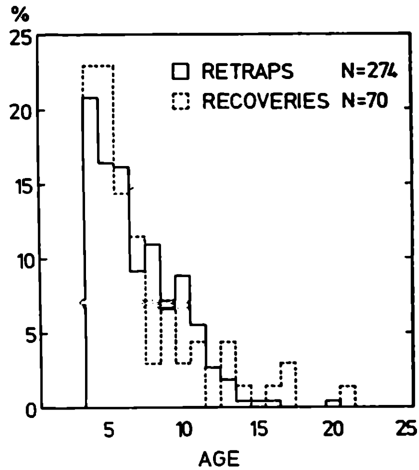

Fig. 13: Relative age distribution of recoveries and retraps of Danish Sandwich Terns.

Survival estimates fall in the range 0.75—0.84 among 2y birds and in the range 0.65—0.83 among 3y terns (Table 8). These values are comparable or slightly larger than those of the adult age classes. Adults are recovered especially during the breeding period and during post-breeding dispersal (July-September) (Fig. 11). The possibility to use recovery data for survival calculations has been tested using two independent samples of recoveries, viz. live retraps of adult breeding birds at Danish breeding grounds during a long-term population study conducted by the Danish Tern Group and recoveries from other sources. The age distribution of 4y+ birds (younger terns are only rarely caught in the colonies, and then only those aged 2—3y) retrapped at the breeding grounds and recovered elsewhere were very similar (Fig. 13). If retraps are used to calculate survival assuming that the birds have reached a stable age distribution, then the result (0.749 ± 0.013 (estimate ± s. e.), N = 274) is very similar to the estimate calculated from recoveries (0.748 ± 0.021 (estimate ± s. e.), N = 70).

The adult survival estimates for the four populations are very similar (0.70—0.75, Table 8). Survival estimates for differently aged birds fall within the interval 0.56—0.80. No significant trends in survival rates have been found. Temporal changes in adult survival rates of birds ringed in different periods are shown in Table 9. Both German and Dutch Sandwich Terns showed marked decreases in Survival between the periods 1910—1939 and 1955—1959, and an increase was seen for German terns between

Table 9: Adult survival estimates for Sandwich Terns ringed in different periods. Estimate ± s. e. Numbers in brackets indicate numbers of recoveries. If less than 20 recoveries are available, no estimate has been calculated.

	Period		
Area	1910—1939	1955—1959	1960—1964
Denmark	.710 ± .045 (29)	.786 ± .038 (25)	.745 ± .036 (38)
Germany	.706 ± .027 (85)	.581 ± .046 (49)	.717 ± .023 (108)
Netherlands	.820 ± .034 (23)	.462 ± .069 (28)	
British Isles	.664 ± .046 (36)	.738 ± .030 (55)	.739 ± .017 (179)

1955—1959 and 1960—1964. Mortality factors may influence survival estimates when causes of mortality affect various age classes differently. Survival estimates based on birds shot are low (Table 10), whereas differences between trapped birds and birds 'found dead' are insignificant. These latter survival rates are deviating to some extent from the estimates obtained by use of all recoveries (Tables 8, 10).

Table 10: Adult survival estimates for Sandwich Terns from different recovery data. Estimate ± s. e. Numbers in brackets indicate numbers of recoveries. If less than 20 recoveries are available, no estimate has been calculated. Recoveries from 1910—1964.

	Cause of recovery		
Area	Shot	Trapped	Found dead
Denmark	.699 ± .043 (34)	.791 ± .039 (23)	.762 ± .029 (51)
Germany	.500 ± .069 (26)	.673 ± .032 (71)	.661 ± .031 (79)
Netherlands			.636 ± .036 (67)
British Isles		.720 ± .030 (63)	.741 ± .021 (112)

6.2. Discussion

Biased age distributions may lead to biased survival estimates. Different geographical distributions of juvenile, immature and adult Sandwich Terns affect the reporting probabilities of recovered birds and thus the age distributions. Survival estimates of the first years are therefore not comparable to each other or to the adult estimates. However, the age distribution of retrapped and recovered adult terns in Denmark was similar (Fig. 13) indicating that recovery age distributions can be used for survival calculations.

Ringing dates can together with ringing dates of birds recovered give rise to estimates of breeding success in different parts of the breeding season. A necessary precondition is that pulli are ringed at the same age throughout the breeding season. During the late part of the breeding season old pulli may be ringed more often than during the early part. The excess of recoveries in July among Danish Sandwich Terns may be due to this effect (Fig. 8). The surplus of recoveries in the early breeding season may be real as the breeding season of Danish terns is earlier than that of the other populations Table 1). A surplus of 'loco' recoveries in Denmark late in the breeding season and early in the breeding season of British Isles terns may be interpreted in a similar way (Figs. 9—10): Danish Sandwich Terns breed early and British Isles terns breed late, and excess of colony recoveries outside these periods may be due to unfavourable conditions. Deviations between 'loco' and other age class ringing date distributions are significant for all age classes. However, differences in ringing date distributions of various age classes recovered outside the colony area are small, and only one difference is statistically significant, viz. adult British Isles birds have been ringed later than juvenile birds. Generally, the effects of breeding time on later suvival can be found before fledging, whereas later effects are small. If most Sandwich Terns breed during favourable food conditions, then surplus recoveries outside the main breeding period may be due to under-nourishment.

The apparent increase in juvenile recovery rates may be due to several factors like an increasing tendency to trap ly Sandwich Terns for food in Africa, or an increased educational level and a decreased illiteracy may have caused a rise in the recovery rates. However, a sudden rise during the 1960's and 1970's can perhaps not be explained from that point of view. A change in the distribution of mortality between age classes may have taken place on a long-term scale. In recoveries, there are several indications of a spatial change in distribution in winter during the present century (Møller 1981—1982). British Isles birds have to an increasing extent been reported from the areas where trapping for food is widespread. This may lead to an increased trapping success, and thus a higher recovery rate. Finally, the effects of sardine fishery upon mortality have to be taken into consideration. Sardine populations in the Gulf of Guinea fluctuate violently. During peak years vast amounts of fish are caught. A large fishery makes bait for trapping easily available to children, and as the terns are present, large numbers are recovered in these years (Dunn & Mead 1981).

From an evolutionary point of view Diamond (1978) has argued that the limiting mortality takes place in the winter quarters outside the breeding season in migratory (tropical) seabirds. To a certain extent this may be true in the British Isles Sandwich Terns, but this species is probably to a large extent affected by human persecution changing the original 'natural' mortality patterns.

Differing survival rates may be off-set by changes in reproductive output among bird species (e. g. Hamilton 1966, Williams 1966). In fact an increase in clutch size has been recorded in Danish Sandwich Terns during the present century. While most terns had a clutch of one egg in the 1930's (1.11 ± 0.32 eggs (av. ± s. d.), N = 1354, (Løppenthin 1939)), many birds have two egg clutches in the 1970's (1.44 ± 0.52 eggs, N = 614, own observations). The difference is a third egg. When comparisons are made with the corresponding survival data no differences in the predicted direction can be seen. Probably so many factors affect the survival estimates that use for purposes like life history is not adequate.

7. Summary

The breeding season showed a trend of increasing retardation from Sweden to the British Isles. The length of the breeding period decreased from Sweden to the Netherlands (Table 1, Fig. 1).

Ring wear is shown as weight decrease in Figs. 2—4. Similar decreases are found in weight with increasing age in Sandwich Tern rings from Denmark and the Netherlands. The legibility of the rings is good, ring wear probably only to a slight degree affecting reporting probabilities of especially old (above 10 years) Sandwich Terns.

Causes of death differed between populations, age classes, seasons, time periods, and recovery areas (Tables 2—4). British Isles Sandwich Terns are trapped to a greater extent than others, while German and especially Danish birds are shot.

Mothly variations show high rates of trapping in winter and high rates of shooting in autumn (and winter) (Figs. 5—7).

Shooting has decreased in importance as a mortality factor, whereas trapping and birds 'found dead' have increased (Table 3).

Shooting is widespread in W and N Europe and trapping is so in W Africa and the Gulf of Guinea (Table 4).

Pre-fledging mortality following ringing is high (Table 5). Breeding success in Denmark is high in May and early June and in July (Fig. 8).

Pre-fledging mortality is low in May-June and high in July-August in Danish Sandwich Terns. In the British Isles population mortality is high in May-June and low in July (Figs. 9—10). Ringing dates of birds recovered in different age classes appeared to show an advantage of early breeding in Denmark and an advantage of late breeding in the British Isles (Table 6).

British Isles Sandwich Terns showed a low juvenile mortality (Table 7). Survival rates were low in juvenile birds (Table 8). The British Isles population showed a seasonal recovery pattern different to that found in the continental populations caused by a different spatial distribution (Fig. 11). A slightly increasing recovery rate in juvenile terns is indicated for the Danish population (Fig. 12).

14—20 % were recovered as immature Sandwich Terns. The seasonal pattern was adult-like at an age of 3y, but not at an age of 2y (Fig. 11).

Adults comprised 13—35 % of recoveries with many recoveries in the Dutch and especially the British Isles population (Table 7). Similar seasonal recovery patterns with many summer recoveries were found at all ages (Fig. 11).

The age distributions of birds recovered and birds retrapped in Danish colonies were similar (Fig. 13). Survival estimates were similar in the four populations (Table 8). Survival rates may have changed during the present century (Table 9). Causes of recovery affect survival rates of adult Sandwich Terns only to a slight degree (Table 10).

8. Zusammenfassung

Brutperiode, Fundumstände und Überlebensrate europäischer Brandseeschwalben *Sterna sandvicensis.*

Die Untersuchung beruht auf der Auswertung der Ringfunde europäischer Brandseeschwalben.

Die Brutsaison der Brandseeschwalbe verspätete sich zunehmend von Schweden in Richtung britische Inseln. Die Länge der Brutperiode nahm von Schweden in Richtung Niederlande ab (Tab. 1, Abb. 1).

Der Ringverschleiß ist in Abb. 2—4 als Gewichtsabnahme dargestellt: Ringe dänischer und niederländischer Brandseeschwalben wiesen vergleichbare Gewichtsabnahmen mit zunehmendem Lebensalter auf. Die Lesbarkeit der Ringe war gut, und Ringverschleiß beeinflußte wahrscheinlich nur in geringem Maße die Wiederfundwahrscheinlichkeit besonders alter Brandseeschwalben (über 10 Jahre alt).

Die Todesursachen variierten zwischen Populationen, Altersgruppen, Jahreszeiten, Beringungszeiträumen und Wiederfundgebieten (Tab. 2—4). Brandseeschwalben der britischen Inseln wurden häufiger gefangen, während deutsche und dänische Vögel häufiger geschossen wurden. Hohe Fangraten ergaben sich im Winter, hohe Abschußraten im Herbst und Winter (Abb. 5—7). Abschuß verlor im Verlauf des Jahrhunderts an Bedeutung als Mortalitätsfaktor, während Fang- und Totfund zunahmen (Tab. 3). Abschuß war in West- und Nordeuropa, Fang in Westafrika und im Golf von Guinea weit verbreitet (Tab. 4).

Bei dänischen Brandseeschwalben erreichte die Kükenmortalität (vom Beringungsalter bis zum Flüggewerden) im Juli/August, auf den britischen Inseln dagegen im Mai/Juni ihr Maximum (Abb. 9—10). Eine Aufgliederung der Funde nach Beringungsmonaten und Altersklassen deutete einen Vorteil für früheres Brüten in Dänemark und für späteres Brüten auf den britischen Inseln an (Tab. 6).

Erstjährige Brandseeschwalben der britischen Population unterlagen geringerer Mortalität (Tab. 7), die bei Jungvögeln allgemein hoch war (Tab. 8). Die jahreszeitliche Wiederfundhäufigkeit der britischen Population unterschied sich von der der kontinentalen Populationen, bedingt durch unterschiedliche räumliche Verteilung (Abb. 11). Die Wiederfundrate dänischer Jungvögel stieg während der vergangenen 50 Jahre andeutungsweise an (Abb. 12).

14—20 % der Wiederfunde entfielen auf 2—3jährige Vögel. Die jahreszeitliche Fundhäufigkeit 3jähriger Brandseeschwalben entsprach derjenigen der Altvögel, im Gegensatz zu dem verzeichneten Fundmuster 2jähriger (Abb. 11).

Altvögel, 13—35 % der Funde, stellten in den Populationen der Niederlande und der britischen Inseln einen höheren Anteil an den Gesamtfunden als in den anderen Populationen (Tab. 7). Alle Altersstufen wiesen ähnliche jahreszeitliche Muster der Fundhäufigkeit mit einem Gipfel im Sommer auf (Abb. 11).

Die Altersverteilungen auf Grundlage der Wiederfunde und der Wiederfänge in dänischen Kolonien waren vergleichbar (Abb. 13). Keinen Trend mit zunehmendem Alter ließ die geschätzte Überlebensrate erkennen, die bei den 4 untersuchten Populationen ähnlich hoch war (Tab. 8). Während dieses Jahrhunderts dürften sich die Überlebensraten verändert haben (Tab. 9). Die Überlebensrate adulter Brandseeschwalben wurde durch die Fundumstände nur in geringem Maße beeinflußt (Tab. 10).

9. References

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