A contribution to the population dynamics of the Common Tern (*Sterna hirundo*) in the Netherlands

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1 *Introduction*

The quality of various water systems is giving cause for concern in many countries. The Dutch Ministry of Transport, Public Works and Water Management has selected the Common Tern *Sterna hirundo* as one of the organisms of which the population size may be indicative of the situation of these systems. The population dynamics of these organisms is studied for management purposes (Schobben 1991). Several authors have stressed the importance of knowledge of bird population dynamics for management and conservation purposes (Croxall & Rothery 1991, Green & Hirons 1991, Jouventin & Weimerskirch 1991, Perrins *et al.* 1991).

To understand the population dynamics of a species, knowledge of the demographic parameters and their interactions is essential. Several methods have been developed to estimate the most important parameters (Clobert & Lebreton 1991). However, one should be aware of the plasticity of the parameters (Perrins 1991). The interactions of the parameters and their effects on the population can be studied by mathematical modelling (Lebreton & Clobert 1991, Danchin 1992). By the National Institute of Coastal and Marine Management (RIKZ), the Leslie-matrix (Leslie 1945, 1948) has been chosen to model the population dynamics of various species (Van Boven & Schobben 1992, Schobben *et al.* 1992). The Leslie matrix has already been shown to be very useful in several studies (Danchin & Monnat 1992, Migot 1992). Mortality and reproduction are the most important parameters for the model. The age composition of a population is an other important parameter because mortality and reproduction vary with age (Chabrzyk & Coulson 1976, Coulson & Wooler 1976, Hays 1978, Nisbet *et al.* 1984).

The dataset of the Euring Data Bank has been used to estimate several demographic parameters. This stresses the importance of national ringing schemes (as already mentioned by Davis 1951 and Van Noordwijk 1993, 1994). Measurements taken during ringing activities in the Delta area in the Southwest Netherlands have been used to study differences between the sexes of the Common Tern. This paper takes a critical look at the ways the various parameters are estimated.

This study was carried out as a practical training during April and October 1995 at the National Institute of Coastal and Marine Management at Middelburg. It was part of my study Biology at the University of Amsterdam.

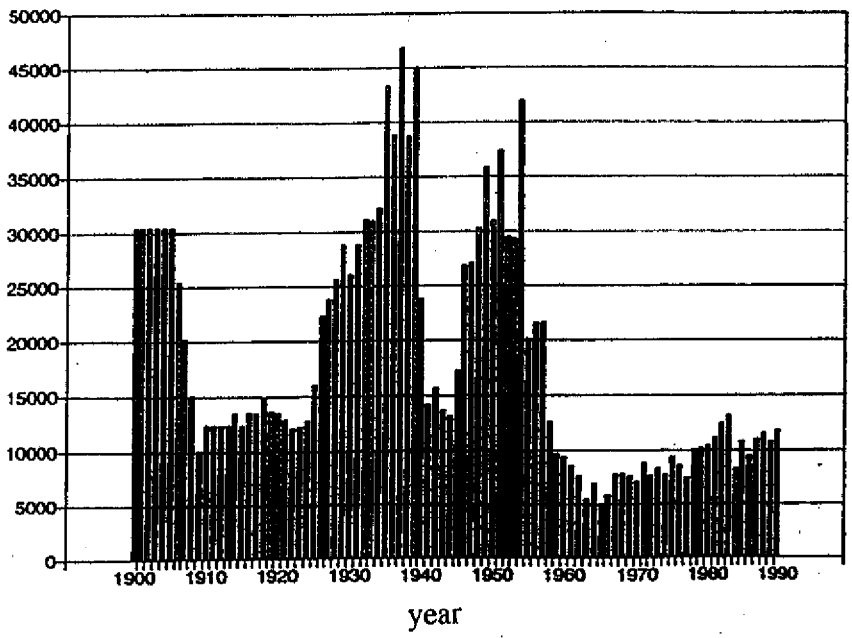
2 *Population development*

Data on the population size of the Common Tern in the Netherlands have been assembled by SOVON, RIKZ and IBN-DLO (Kwint 1992, Stienen & Brenninkmeijer 1992). For the purpose of this study, only data on the breeding population along the Dutch coast have been analysed. The total number for the entire country is several hundred breeding pairs higher.

At the beginning of this century, the breeding population of the Common Tern along the Dutch coast numbered more than 30,000 pairs (fig 1). Between 1905 and 1910, the population declined strongly, owing to the shooting of adult Common Terns for the millinery and of the taking of eggs. After 1910 the species was declared protected and the numbers increased slowly. By 1930 the coastal population had grown to about 26,000 breeding pairs. The colonies were found mainly in the Southwest and in the Waddensea-area. For the period since 1930 sufficient information is available to make a reliable reconstruction of the development of the population. It appears that the number of breeding pairs along the Dutch coast increased strongly between 1930 and the Second World War. In 1939, there were slightly more than 45,000 breeding pairs along the coast. During the war, the numbers decreased again to 17,200 pairs, on account of the shooting of adult birds, the collecting of eggs and other forms of disturbance. After 1945, the population increased to over 30,000 pairs in 1948. At the end of the 1950's, the species decreased enormously down to its lowest ebb in 1965, when the total population was no more than about 5,000 breeding pairs. This reduction took mainly place in the coastal areas and was caused by poisoning with chlorinated hydrocarbons, which were spread by a factory along the Nieuwe Waterweg. After this extreme low, the breeding population recovered to about 10,000 pairs in the last twenty years. In 1983, the population consisted of slightly more than 13,000 pairs, in 1990 almost 12,000. The population level from before the poisoning incident has not been reached yet. At this moment, most Common Terns are breeding in the Delta-area (more than 40% of the Dutch population) and the Waddensea-area (almost 37% of the Dutch population).

Figure 1: Reconstructed population development of the Common Tern in The Netherlands between 1900-1990 (after Stienen & Brenninkmeijer 1992).

number of breeding pairs



3 *Methods*

3.1 *Survival*

To calculate survival rates, recoveries during 1983-1994 have been selected from the database at the Euring Data Bank. Recoveries with the following finding conditions have been used: (1) Dead but no information on how recently the bird had died; (2) Freshly dead, within about a week; and (3) Not freshly dead, the bird had been dead for more than about a week. The use of recoveries of birds reported freshly dead is preferable to obtain the most accurate results. However, this would yield too few recoveries to run the various models. Fortunately delayed reporting has only little effect on survival estimates (Anderson & Burnham 1980). The recovery period runs from 1 May in one year to 1 May in the next year. This runs more or less parallel to the age in years of the birds, which makes it more natural than the use of calendar years. The exact date of 1 May has been suggested by J.H.M. Schobben, mathematical biologist of RIKZ. The first of May was also used for a population model of the Sandwich Tern, *Sterna sandvicensis* (Van Boven & Schobben 1992). Birds from which only the ring was found have been omitted. These birds could have been dead for years. Recoveries of first calendar year birds have been included only when the distance to the ringing area was more than 5 km. This made it possible to calculate post-fledging survival rates. Survival rates before fledging can not be calculated accurately because: (1) The ringed sample is not representative. Mortality rates among chicks are extremely high (Langham 1972). To waste as few rings as possible, many ringers ring only the stronger chicks, wich have the greatest chance of survival. These are very often the older chicks. (2) Many ringers do not report dead chicks, even if the chicks had been ringed already. Recoveries of second calendar year birds which were ringed as young and were recovered in Europe are considered erroneous and have been omitted. Common Terns stay in the wintering areas during their second calendar year (Mead 1971, Cramp 1985).

Recoveries during the period 1983-1994 have been used to compose datasets (see table 4.1-4.6). The computer programme BROWNIE from Brownie *et al.* (1985) has been used to analyse these sets.

3.2 *Mean life span*

Brownie *et al.* (1985) provided a formula for the calculation of the mean life span for birds ringed as young:

$$E(T) = \frac{1}{-ln(S')} + \frac{S'}{-ln(S)} + \frac{S'}{ln(S')}$$

Where *E(T)* = life expectancy in years, *S'* = survival rate during the first year of life, *S* = annual survival rate after the first year of life. For the mathematical derivation of the formula, see Brownie *et al.* (1985).

3.3 *(Mean) Age composition*

For the calculation of the age composition of the Common Tern population breeding in the Netherlands, both the database from the Euring Data Bank and records from the Delta-area in 1995 have been used. Only individuals found dead, recaptured or resighted in breeding colonies were selected from the database of ringing recoveries. Records outside the breeding season (15 May - 31 July) were omitted. The reason for doing so is to omit as much as possible records of prospecting and migrating birds. Individuals ringed as nestling, of which the exact age was known, and found dead, recaptured or resighted in the colonies were selected from the database. Birds of one year old were omitted because Common Terns stay in the wintering areas during their first breeding season (Mead 1971, Cramp 1985).

In 1995, birds were captured in breeding colonies in the Delta area. Most birds were trapped at the nest, a few were captured by mistnetting, a single bird was found dead. Under the assumption that these birds form a representative sample of the Dutch population, they were added to the database records.

The records were corrected for ringing effort in the year in which the birds had been ringed. This was attained by dividing the records by the number of young ringed in the year of origin.

The records were corrected for ring-loss. Hatch & Nisbet (1983a) published an article about ring-loss in Common Terns. According to them, the first rings begin to fall off in the sixth year and half will be lost by the twelth year. The eldest Common Tern recorded in the Euring Data Bank reached the age of 19 years. Based on these assumptions, the following function for ring-loss has been calculated during the present study: $Y = 144.69 - 7.6772 \times X$. Y represents the percentage of rings still attached to a birdlegg and X represents the time since ringing. For every age-class, the percentage ring-loss has been calculated. These percentages have been used to correct the results of each age-class found for the age composition.

3.4 *Age at first breeding*

The age at first breeding can be calculated if the age composition and the mean adult mortality are known. The mean adult mortality can be calculated as 1 minus the mean adult survival. One assumption that must be made is that the age composition is constant over the years under study. This is the case for the mean age composition, calculated in chapter 3.3. In nature, the age composition will not be constant and neither will the age at first breeding.

All the birds at age 2 (in their 3rd calendar year) are first breeders. The amount of first breeders at age 3 can be calculated as the total number of birds at age three minus the birds breeding at age 2 multiplied with the mean adult mortality. The amount of first breeders at age 4 can be calculated by the total numbers of birds at age 4 minus all those breeding at age 3 multiplied with the mean adult mortality. This can go on as long as the numbers breeding at age $i + 1$ is larger than age $i \times$ the mean adult mortality.

3.5 *Survival until first breeding*

The survival until first breeding can be calculated from the age at first breeding and the survival rates.

First year survival rate, from fledging until age 1, is calculated according to the method given in 3.1. The total juvenile survival rate incorporates also fledgingsucces. The mean value of the fledging success of Griend has been used for further calculations.

The survival until first breeding depends on the age at first breeding. Birds that breed at age 2 (in their 3rd calendar year) have a survival of fledging success (F) * first year survival from fledging (S') * adult survival (S). Birds that breed at age 3 have a survival of $FS'S^2$, and so on. The weighed survival until first breeding can be calculated by the sum of the proportion of birds breeding for the first time at age n multiplied by the survival of birds breeding for the first time at age n.

3.6 *Age related dispersal*

To study distance and direction of dispersal, birds reported during the breeding season from breeding colonies, dead or alive, were selected from the database of the Euring Data Bank. Birds from which only the ring was found were omitted. From birds with double records, only the records showing the largest distance of dispersal were selected. The data were separated in birds ringed as young and birds ringed as adults. From the birds ringed as adults, only the birds which were reported at least one year after ringing were selected. This has been done in order to omit recaptures in the same breeding season, which would result in most of the cases in direction and distance zero. This would result in a bias in distances and directions of birds ringed as adults with regard to birds ringed as young.

The dispersal distances from birds ringed as young and birds ringed as adults are divided into groups of twenty-five kilometres. The median has also been calculated. The difference was tested with a Median Test.

For each of the eight wind-directions, the number of birds which displayed dispersal were counted, separately for birds ringed as young and birds ringed as adult.

3.7 *Separating the sexes*

During ringing activities in the Delta area between 1984 and 1995, 472 adult Common Terns were caught of which total head length was measured. The measurements were obtained using a slide-rule (fig 2) and are rounded to the nearest 0.1 mm. Almost all the measurements were taken by one person, so the effect of intra-observer variability as described by Barrett *et al.* (1989) is negligible.

A discriminant value for the total head length of the sexes of the Common Tern has been established using a probability plot. A normal distribution on a probability plot results in a straight line. The two normal distributions, of male and female total head lengths, should result in a sigmoid curve. The point of inflexion indicates the discriminant value. This method was used by Coulson *et al.* (1983) for sexing Herring Gulls. Their results of the probability plot were very close to the results of a discriminant analysis.

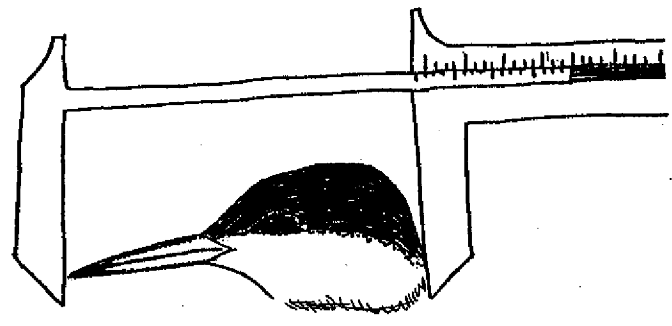


Figure 2: The measurement of the total head lenghth of a Common Tern using a slide-rule.

A sample of total head lengths of twelve birds of known sex, four males and eight females, has been used to obtain a rough indication of the reliability of the discriminant value obtained in the probability plot.

3.8 *Sex related dispersal*

If the discriminant value is known, it is possible to study some sex-related differences in several variables of interest. For population dynamics, dispersal is of particular interest. The dispersal distance of each sex is estimated by the median value. The median value is a more useful measure than the mean value because dispersal distances are skewed towards the point of origin (Greenwood & Harvey 1982). The medians were only calculated for birds ringed as nestling. Birds ringed as adult have on average lower dispersal rates, so both age-groups can not be analysed together. However, there are not enough data available to calculate median dispersal values for birds ringed as adults. To study differences in the dispersal direction between the sexes, the method described in chapter 3.6 is applicable.

Although most of this report is based on data assembled in the whole of The Netherlands, the total head length measurements were taken from birds of the Delta area only. This includes measurements taken during the breeding season of 1995. Any difference resulting from this restriction is assumed to be inconsequential.

4 *Results*

4.1 *Survival*

The available recoveries from the database of the Eurring Data Bank are shown (table 4.1 and 4.2) in the format recommended by Brownie *et al.* (1985).

Table 4.1: Recoveries during 12 years of Common Terns ringed as adults in The Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years) 1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1983	489	1	0	0	0	1	0	1	0	0	0	0	0
1984	361		0	0	1	1	1	0	0	0	0	1	0
1985	108			0	0	0	0	0	1	1	0	0	0
1986	76				0	0	0	0	1	0	0	0	0
1987	81					0	0	1	1	0	0	0	0
1988	175						0	0	1	0	1	0	0
1989	81							0	0	0	0	0	0
1990	175								0	2	1	0	0
1991	243									1	0	0	0
1992	153										0	0	0

Table 4.2: Recoveries during 12 years of Common Terns ringed as young in The Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years) 1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1983	3232	10	0	1	3	0	0	0	0	0	0	0	0
1984	1993		6	0	1	1	1	0	0	1	1	0	1
1985	1415			1	0	1	0	1	0	0	2	0	0
1986	3942				9	1	2	2	3	1	0	0	0
1987	2827					4	3	0	3	1	1	2	1
1988	4697						7	1	2	2	1	0	0
1989	2579							10	3	0	2	0	2
1990	1203								4	0	0	0	1
1991	2519									2	0	0	0
1992	2718										0	0	1

Because there are too few records of recoveries of birds ringed as adult, it was decided to add data on birds recaptured in later seasons. Mardekian & McDonald (1981) developed a method which uses both recoveries and recaptures for estimating survival rates. The method works with recoveries and terminal recaptures, which means that for every bird only the last record is included in the analysis. Only recaptures during the ringing period (i.e. the breeding season) are used. The recaptures in year i are added to the recoveries in the year i - 1. An application of this method on Canada Goose data yielded a mean survival rate which is between that of recoveries and recaptures alone, but has a much smaller standard error (Francis & Cooke 1993).

Records of recaptures of birds during the same season as they were ringed were also omitted. Only recaptures in the Netherlands have been used. This is conform the Mardekian & McDonald method. The matrices according to the Mardekian & McDonald method are shown in table 4.3 and table 4.4. Every reporting period incorporates both the year of recovery as the year of recapture.

Table 4.3: Reportings during 12 years according to the Mardekian & McDonald method for Common Terns ringed as adults in The Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years)											
		1983/ 1984	1984/ 1985	1985/ 1986	1986/ 1987	1987/ 1988	1988/ 1989	1989/ 1990	1990/ 1991	1991/ 1992	1992/ 1993	1993/ 1994	1994/ 1995
1983	489	3	1	0	0	1	0	1	0	0	0	0	0
1984	361		2	2	1	2	2	1	0	1	0	3	0
1985	108			0	0	0	0	0	1	2	0	0	0
1986	76				0	0	1	0	1	0	0	0	0
1987	81					0	0	1	2	2	0	0	0
1988	175						0	2	1	0	1	0	0
1989	81							1	0	2	0	0	1
1990	175								3	5	2	0	0
1991	243									3	3	0	0
1992	153										3	2	1

Table 4.4: Reportings during 12 years according to the Mardekian & McDonald method for Common Terns ringed as young in The Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years)											
		1983/ 1984	1984/ 1985	1985/ 1986	1986/ 1987	1987/ 1988	1988/ 1989	1989/ 1990	1990/ 1991	1991/ 1992	1992/ 1993	1993/ 1994	1994/ 1995
1983	3232	10	1	2	7	1	0	1	1	0	0	0	0
1984	1993		6	3	5	3	2	1	2	1	1	0	1
1985	1415			1	1	7	4	1	2	0	2	0	1
1986	3942				9	7	6	3	6	1	1	0	2
1987	2827					4	4	1	8	1	1	2	2
1988	4697						7	4	3	3	3	0	4
1989	2579							10	4	3	2	3	8
1990	1203								4	0	0	1	2
1991	2519									2	3	0	4
1992	2718										0	1	5

The data assembled according to the Mardekian & McDonald method provided also too few data to run the models of BROWNIE. The database of the Euring Data Bank contains not only recaptures during the breeding season. There are also recaptures from the areas along the migration routes and from the wintering areas. In table 4.5 and 4.6 recoveries and recaptures from all months of the year have been added together. The reporting rate f in table 5.2. is now a combined recovery and recapture rate. Like in the study of Mardekian & McDonald (1981) these rates cannot be estimated separately.

To calculate post-fledging survival only recaptures of first calendar year birds have been selected if the distance to the ringing area was more than 5 km. Recaptures of adult birds during the same year as they were ringed, were selected only if the distance to the ringing area was not 0.

Table 4.5: Summed recoveries and recaptures during 12 years for Common Terns ringed as adults in The Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years) 1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1983	489	1	3	2	0	1	1	2	0	0	1	0	0
1984	361		2	4	1	1	2	1	1	0	1	1	2
1985	108			4	0	1	0	0	1	1	1	0	0
1986	76				1	0	0	1	1	0	0	0	0
1987	81					0	0	1	1	1	2	0	0
1988	175						1	1	3	0	1	0	0
1989	81							0	1	0	2	0	0
1990	175								1	5	4	1	0
1991	243									7	3	3	0
1992	153										1	2	2

Table 4.6: Summed recoveries and recaptures during 12 years for Common Terns ringed as young in the Netherlands between 1983-1994

Year ringed	Number ringed	Reporting period (in years) 1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994
1983	3232	23	1	2	4	6	1	0	4	1	1	0	0
1984	1993		17	2	7	6	6	2	4	4	3	1	1
1985	1415			9	2	3	8	7	1	3	3	0	1
1986	3942				22	2	9	8	8	7	1	3	0
1987	2827					3	4	2	7	8	3	3	1
1988	4697						23	3	13	6	2	3	2
1989	2579							19	4	1	6	1	5
1990	1203								10	0	0	0	2
1991	2519									5	0	3	0
1992	2718										9	0	2

Fortunately, the joint recoveries and recaptures produced sufficient data to run the models. The main conclusions of the output can be summarized as follows:

The Likelihood Ratio Test that compares the H_{01} model with the H_{02} model shows that the H_{01} model is rejected in favour of the H_{02} model ($\chi^2 = 73.73$, d.f. = 20, $P < 0.001$). Recovery rates are not constant from year to year. The Likelihood Ratio Test that compares the H_{02} model with the H_1 model shows that the H_{02} model is rejected in favor of the H_1 model ($\chi^2 = 62.16$, d.f. = 17, $P < 0.001$). So survival rates are not constant from year to year. The next three tests are not Likelihood Ratio Tests, but are analogous to the goodness of fit tests of the various models. The test of H_0 against H_1 results in a rejection of the H_0 model ($\chi^2 = 240.923$, d.f. = 20, $P < 0.001$). Survival and recovery rates are age-dependent. The test of H_1 against H_2 results in a rejection of the H_2 model ($\chi^2 = 16.054$, d.f. = 9, $P = 0.07$). However, before deciding that model H_1 should be used, the goodness of fit tests and the test of H_2 vs. H_3 should also be examined. The test of H_2 against the alternative H_3 results in a rejection of H_2 ($\chi^2 = 25.554$, d.f. = 10, $P = 0.004$). This means that survival and recovery rates are age-dependent for the first two years of life.

The goodness of fit tests of the various models show that only model H_3 fits the data well (χ^2 = 18.84, d.f. = 14, P = 0.2). However, it is not possible to estimate the survival rates under this model. This means that with the given data set, it is impossible to attain reliable estimates of the survival rates.

A possible explanation for the fit of model H_3 could be that reporting rates during the second year of life are much lower than in other years, causing a significant difference in survival estimates. During the second year of life, birds stay in the wintering areas, where they get snared (Allison 1959, Mead 1978) by local birdtrappers. Reportings occur probably at a much lower rate, because it is unlikely that an African boy who snares a Common Tern reports the ring to the Euring Data Bank. To study the effect of this, records of birds in their second year of life are omitted from the matrix. The newly created matrix is again analysed using BROWNIE. Model H_3 was still the only model that fitted the data well. This means that the data in hand are insufficient to reject the possibility that there are age-dependent differences in adult survival. As this appears intuitively unlikely, survival has been calculated using the other models.

For the AMOEBE project and for further calculations (recruitment rates, age at first breeding), it is very important to have some estimate of the survival rates. During the various tests between the models, the H_1 model turned out to be the model that would be chosen if the goodness of fit test was appropriate. However, the survival estimates are too low to be very reliable. Studies of Stercorariidae and other Laridae have shown that an adult mortality of around 10% can be expected (among others Jouventin & Weimerskirch 1991, Croxall & Rothery 1991). The results of the H_{01} and H_{02} model are therefore much more realistic. The assumptions of these models, however, are rarely met in nature. The results of the H_{01} model have been used for further calculations (table 4.7). One should bear in mind that the assumptions of this model are similar to the assumptions of the criticized life table method (see 5.1).

Table 4.7: Results of recovery- and survival rates of adult and young Common terns calculated by the H_{01} model.

Age class	Recovery rate			Survival rate		
	average estimate	standard error	95% confidence interval	average estimate	standard error	95% confidence interval
adult	0.0083	0.0011	0.0062 - 0.0105	0.8676	0.0210	0.8264 - 0.9088
young	0.0050	0.0004	0.0041 - 0.0058	0.1977	0.0257	0.1473 - 0.2481

4.2 *Mean life span*

According to the formula provided by Brownie *et al.* (1985), the mean life span of a Common Tern amounts to 0.39 year.

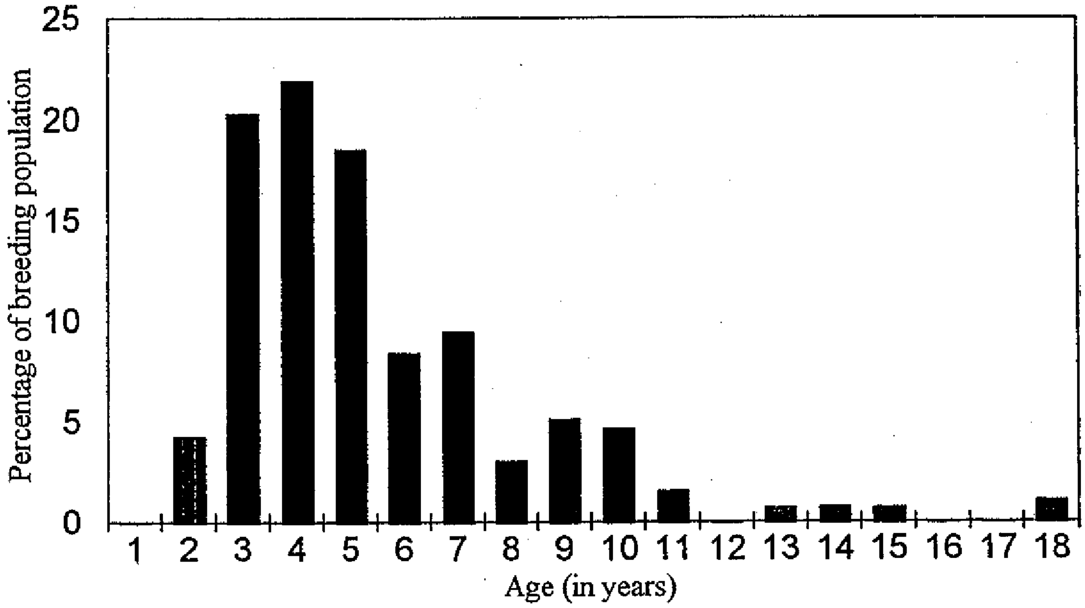
4.3 *Age-composition*

Table 4.8: Age-composition of Common Terns breeding in The Netherlands, corrected and not corrected for ring-loss.

Age-class	N birds found in age-class	N corrected for ringing effort		Percentage ring-loss	N corrected for both ringing effort and ring-loss	
		Total	Percentage		Total	Percentage
2	5	2.15	4.22	0	2.15	3.94
3	22	10.31	20.27	0	10.31	18.93
4	25	11.13	21.89	0	11.13	20.45
5	17	9.41	18.50	0	9.41	17.28
6	11	4.26	8.37	1.37	4.31	7.92
7	12	4.80	9.44	9.05	5.24	9.62
8	4	1.53	3.00	16.73	1.78	3.27
9	6	2.59	5.09	24.40	3.22	5.91
10	5	2.33	4.58	32.08	3.08	5.65
11	2	0.76	1.50	39.76	1.06	1.95
12	0	0	0	47.44	0	0
13	1	0.35	0.69	55.11	0.55	1.00
14	1	0.36	0.70	62.79	0.58	1.07
15	1	0.35	0.69	70.47	0.60	1.10
16	0	0	0	78.15	0	0
17	0	0	0	85.82	0	0
18	1	0.53	1.05	93.50	1.03	1.89

To study if the corrected and uncorrected totals differ significantly, the age classes higher than 10 were pooled. The Chi Square Test shows that the difference between the totals is not significant (χ^2 = 0.55, d.f. = 9, P = 1). If the first five ageclasses, where ring loss is assumed to be negligible, are omitted, the difference between the percentages is still not significant (χ^2 = 0.24, d.f. = 5, P = 1).

Figure 3: Age-composition of Common Terns breeding in The Netherlands, uncorrected for ring-loss.



4.4 *Age at first breeding*

Table 4.9: The share of every age-class in the total amount of new breeders and the percentage new breeders per age-class.

Age-class	Percentage of the new breeders	Percentage first breeders among the age class
2	17	100
3	66	82
4	17	20

It is obvious that most new breeders establish themself at age three, in their 4th calendar year. The amount of first breeders is 25% of the total population, when the figures of the age composition are not corrected for ring-loss.

4.5 *Survival until first breeding*

Table 4.10: The survival until the different ages of first breeding.

Age class	Survival
2	0.060
3	0.052
4	0.045

According to calculations (see 3.5), the weighed survival until first breeding amounts to 0.035.

4.6 *Age related dispersal*

Table 4.11: The numbers of Common Terns ringed as adults and Common Terns ringed as young found at the different dispersal distances.

Dispersal distance (in km)	Birds ringed as young	Birds ringed as adults
0-25	61	47
25-50	14	2
50-75	5	0
75-100	12	0
100-125	1	0
125-150	4	0
150-175	1	0
200-225	1	0
300-325	1	0
350-375	1	0
575-600	0	1
Total	101	50

In order to use a Chi Square Test, the distances over 50 km were pooled. The difference between the dispersal distance of young birds and adult birds is highly significant ($\chi^2 = 18.89$, d.f. = 2, $P < 0.0001$).

Of Common Terns which do exhibit dispersal, the median distance of 75 birds ringed as young amounts to 29 km. The median dispersal distance of 18 birds ringed as adult amounts to 3.5 km. The difference between the two age-classes was tested by a Median Test ($\chi^2 = 8.19$, d.f. = 1, $P = 0.004$). It is obvious that young Common Terns exhibit more dispersal than adult Common Terns.

Table 4.12: The numbers and percentages of Common Terns ringed as young and Common Terns ringed as adult for every dispersal direction.

Dispersal direction	Birds ringed as young	Birds ringed as adults	Percentage birds ringed as young	Percentage birds ringed as adults
N	3	2	4	10
NE	4	1	6	5
E	12	9	18	45
SE	2	1	3	5
S	6	1	9	5
SW	26	2	38	10
W	11	0	16	0
NW	4	4	6	20
total	68	20	100	100

In order to use a Chi Square Test, the records have been rearranged between the four main directions. A NE record is counted as a half record North and a half record East (table 4.13).

Table 4.13: The numbers and percentages of Common Terns ringed as young and birds ringed as adult for every main dispersal direction.

Dispersal direction	Birds ringed as young	Birds ringed as adults	Percentage birds ringed as young	Percentage birds ringed as adults
N	7	4.5	10	29
E	15	5.5	22	35
S	20	2.5	29	16
W	26	3	38	19
total	68	15.5	±100	±100

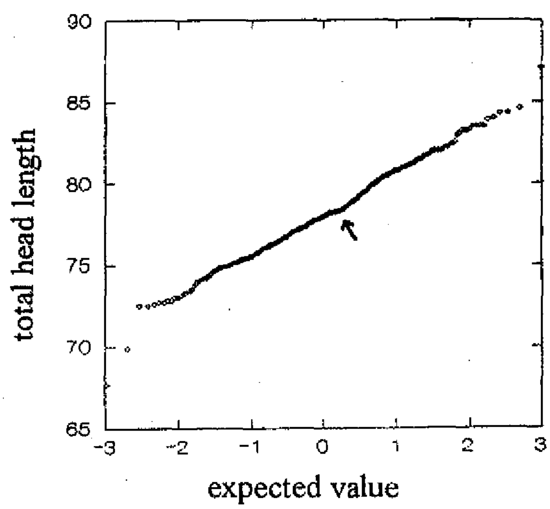
The difference between the dispersal direction of the young and adult birds is not significant ($\chi^2 = 5.7$, d.f. = 3, P = 0.1).

4.7 *Separating the sexes*

The 472 total head lengths are plotted in fig 4. Although the expected two straight lines are not very obvious, there seems to be a point of inflexion at 78.1 mm (see the arrow in fig 4). Total head lengths longer than 78.1 mm should be of males, total head lengths shorter than 78.1 mm should be of females.

The mean values for male and female total head length have been calculated after omitting three extreme values which are probably erroneous. The 'ties' (records of value 78.1) are also omitted. The mean value found for 239 adult female Common Terns amounts to 76.2 ± 1.35 mm. The mean value found for 222 adult male Common Terns amounts to 80.1 ± 1.54 mm. According to these mean values, the total head lengths of males are 4.9% larger than the total head lengths of females.

Figure 4: Total head length measurements plotted on proba bility paper.



The 12 birds of known sex have been used to check the reliability of the discriminant value. Using this value, the sex of 100% of males as well as 100% of females was correctly identified . This gives some confidence in the result of the calculations, although the sample was very small.

4.8 *Sex related dispersal*

The median dispersal distance for 15 female Common Terns amounts to 10 km. The median dispersal distance for 6 male Common Terns amounts to 14 km. According to these median dispersal distances, males disperse further than females. However, the values do not differ significantly (Median Test χ^2 = 0.15, d.f. = 1, P = 0.7).

Table 4.15: The numbers and percentages for every dispersal direction for male and female, ringed as young or adult, belonging to the Delta area, SW-Netherlands.

Dispersal distance	Females, ringed as		Males, ringed as		Percentage females ringed as young	Percentage males ringed as young
	Young	Adult	Young	Adult		
N	3	2	0	0	18	0
NE	1	0	0	0	6	0
E	4	2	0	0	24	0
SE	0	0	2	1	0	20
S	2	0	2	0	12	20
SW	3	0	4	0	18	40
W	3	0	0	0	18	0
NW	1	0	2	0	6	20
Total	17	4	10	1	± 100	100

In order to use a Chi Square Test, the records of the birds ringed as young have been rearranged by dividing them over the four main directions (table 4.15). There are too few records of adult birds of known sex to test the difference between the sexes. A NE record is counted as a half record North and a half record East.

Table 4.15: The numbers and percentages of females and males ringed as young for each of the main dispersal directions.

Dispersal direction	Females ringed as young	Males ringed as young	Percentage females ringed as young	Percentage males ringed as young
N	4	1	24	10
E	4.5	1	26	10
S	3.5	5	21	50
W	5	3	29	30
total	17	10	100	100

The difference between the dispersal direction of male and female birds is not significant ($\chi^2 = 3.4$, d.f. = 3, P 0.3)

5 *Discussion*

5.1 *Survival*

Survival rates, and hence mortality rates, have been calculated for birds since the 1940's. Survival rates were calculated from ringing recoveries using life tables (Lack 1943a, 1943b, 1949). Life table methods are thoroughly described and applied to several species by Hickey (1952). The life table method has been used by numerous scientists all over the world. However, the underlying statistics of this method are poor. Burnham & Anderson (1979) provided a goodness of fit test for the life table method, and tested the method on several waterfowl species. They concluded that the composite dynamic life table method should not be used in the analysis of waterfowl ringing data. Criticism on the assumptions of the method was raised also by several statisticians (Cormack 1970, Botkin & Miller 1974, Burnham & Anderson 1979, Anderson & Burnham 1980, Anderson *et al.* 1981, Lakhani & Newton 1983, Anderson *et al.* 1985). Two assumptions are of primary concern: (1) annual survival is assumed to be age specific only, hence independent of year; and (2) the reporting rate is assumed to be a constant over all ages and years. These assumptions are rarely met in practice. Haldane (1955) computed survival in a statistically satisfactory way, but he also had to make the two mentioned assumptions (Lakhani & Newton 1983, Clobert & Lebreton 1991). During the 1970's, some robust models were developed, involving age- and time-dependent survival and reporting rates. These models are summarized by Brownie *et al.* (1985). These authors also provided two computer programmes for making calculations with several models and testing these mutually.

Another method of calculating survival rates is the use of 'capture-mark-recapture' (CMR). During the 1960's, three statisticians each developed a model for survival calculations by recaptures/resightings of marked animals. The basic structure of the three models was the same and is referred to as the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965). This model forms the basis for survival calculations by recaptures (Clobert *et al.* 1985, Clobert *et al.* 1987, Clobert & Lebreton 1991, Lebreton *et al.* 1992). This method has the weakness that survival rates are almost always underestimated because of birds which moved permanently out of the study area (Clobert & Lebreton 1991). Francis & Cooke (1993) used the term 'apparent survival rate' when the survival rate was calculated by recaptures. They found that the apparent survival rates were indeed generally lower than the survival rates from recoveries.

For every survival study, the use of both methods is probably best. The results can be compared and conclusions can be drawn. In the near future, some robust models which incorporate both recaptures and recoveries may be developed. Some important work on this aspect has already been done (Buckland 1980, Mardekian & McDonald 1981, Buckland 1982, Clobert & Lebreton 1991).

The Euring Data Bank contains relatively few recaptures and resightings of Common Terns from The Netherlands. Most of the records concern birds reported dead. Common Terns that have been recaptured or resighted more than once, in different years, are rare. So the possibility of using CMR for estimating survival rates is out of the question. Consequently, only the models of Brownie *et al.* (1985) could be used (table 5.1). The basic structure of the models depends on three parameters: the numbers ringed in a given year, the reporting rate, and the survival rate (table 5.2).

Table 5.1: List of the models in the programme BROWNIE for birds ringed as young and adults with their assumptions.

Model	Assumptions
H_{01}	(1) young and adult birds have different survival and recovery rates; and (2) otherwise, survival and recovery rates are constant from year to year.
H_{02}	(1) young and adults have different survival and recovery rates; (2) survival rates are otherwise constant from year to year; and (3) recovery rates are year-specific.
H_0	(1) survival and recovery rates are year-specific but age-independent
H_1	(1) annual survival and recovery rates are year specific; and (2) young birds have different survival and recovery rates from those of adults
H_2	(1) annual survival and recovery rates are year specific; (2) young birds have different survival and recovery rates from those of adults; and (3) in any year, the recovery rate for newly released birds is different from that for survivors of previous releases, and hence the corresponding recovery rates are different
H_3	(1) annual survival and recovery rates are year-specific (2) survival and recovery rates are age-dependent for the first two years of life (this embraces assumption (3) of H_2 for the type of data being analysed).

Table 5.2: Basic structure of the models.

Ringing occasion	Number ringed	Period of recovery			
		1	2	3	4
1	N_1	N_1f	N_1Sf	N_1SSf	N_1SSSf
2	N_2		N_2f	N_2Sf	N_2SSf
3	N_3			N_3f	N_3Sf

Where: f = reporting rate, S = survival rate

Using the models of Brownie *et al.* has some benefits. They are well developed and have been tested. Since the beginning of survival studies, the problem of ring-loss and its effects on survival rates has been recognised (Hickey 1952, Austin & Austin 1956, Botkin & Miller 1974, Nisbet 1978, DiCostanzo 1980). Several studies have been dedicated to the subject (see for example Coulson & White 1954, Harris 1964, Ludwig 1967, Harris 1980, Perdeck & Wassenaar 1981, Hatch & Nisbet 1983a, 1983b, Nisbet & Hatch 1983). The models of Brownie *et al.* have been tested for ring loss by Nelson *et al.* (1980). They simulated several degrees of ring loss and found that estimates of annual survival rates were only slightly negatively biased in most cases.

The effects of delayed reporting rate of ringing recoveries on the estimators of the models of Brownie *et al.* have been tested by Anderson & Burnham (1980). They found that the estimates of most models are slightly positively biased because of delayed reporting.

There are no models which can accurately estimate survival rates from ringing recoveries from birds ringed as young only. Recoveries from birds ringed as adults are also needed (Anderson *et al.* 1985, Brownie *et al.* 1985). Lack (1946) showed that adult survival differs from first year survival in many species. This has been confirmed in innumerable later studies and is certainly also the case for the Common Tern. Therefore it is important to estimate first year survival, which demands recoveries from birds ringed as downy young. Recoveries of birds ringed as young are relatively abundant in the Dutch material. However, there are only a few recoveries from birds ringed as adults. Almost all these records are from after 1982, so this period has been used for estimating survival rates.

Although the estimates of the survival rates in table 4.7 are the best available estimates for the Dutch population at this time, they are approximate only. The goodness of fit test of the H_{01} model indicates that the model cannot be used. And there are some other problems with these estimates. The numbers of ringed birds in a given year were provided by the Euring Data Bank, but without an estimated accuracy that the reported numbers were indeed the correct numbers (pers. comm. R. Wassenaar). The actual numbers in some years could differ from the given numbers, due to the change-over to computerized analysis at the ringing centre. This effects the survival estimates. The Euring Data Bank could not provide exact numbers of adult birds ringed in a certain year. They recorded the numbers of full-grown birds ringed in a certain year. This number includes first calendar year Common Terns ringed outside the breeding season and migrating adults. The recovery and recapture probabilities of these birds differ from adult birds ringed during the breeding season. Birds ringed away from the breeding colonies are not included in the recovery matrices. They should also not be included in the total numbers on ringed adults in a given year, but they are. The recoveries file shows the amount of adult birds ringed in the breeding season and the rest of the full-grown birds for the different years . It is not possible to use this ratio as an estimate for the total amount of adults ringed during the breeding season, because the recovery rates differ between the different groups. First calendar year birds have a lower survival, migrating adults have much lower recapture probabilities. So the actual estimates of adult survival are almost certainly higher than those estimated with BROWNIE.

Several authors have estimated adult mortality of the Common Tern. Austin & Austin (1956) estimated an annual adult mortality of 26.1 - 26.3%. They used the dynamic life table method. Großkopf (1964) estimated a mortality of 19%. He used the time specific life table method. Nisbet (1978) used parameters as annual recruitment rate, net annual immigration rate and annual decrease in population, and combined it with recaptures. In doing so, he inferred an annual adult mortality of 13 - 21%. DiCostanzo (1980) used methods analogous to life tables and found adult mortality rates of 8.0% and 9.2%.

The estimates of mortality found during this study are more or less in agreement with the findings of Nisbet and DiCostanzo. They are also in agreement with the findings of other seabirds (Jouventin & Weimerskirch 1991, Croxall & Rothery 1991). However, they are much lower than the findings of Großkopf and Austin & Austin. DiCostanzo claimed that the high mortality rates found by Austin & Austin and by Nisbet were due to combining data of several colonies. This would include small, unsuccessful and relatively unstable populations. By taking the Netherlands as one population, the data of numerous colonies have been combined in this study. I don't agree with DiCostanzo that this should result in a high estimate of adult mortality. If the overall population is stable, the few declining colonies should not have a significant effect on the overall mortality rates, unless the majority of the data comes from these colonies. Normally, the effects of declining colonies will be counteracted by the effect of increasing colonies.

5.2 *Mean life span*

Although Dutch Common Terns can reach the age of 19 years (according to the records at the Euring Data Bank), the estimated mean life span is very low. This is mainly due to the fact that the mean life span in this study is calculated from the moment of fledging, and a great deal of the losses are suffered shortly after fledging. Großkopf (1964) calculated a life expectancy of 6.8 years. DiCostanzo (1980) calculated that birds that survive until age 4 have a life expectancy of 12 years, which is in agreement with his low estimate of annual adult mortality. Both values are too high because the survival of young birds is not taken into acount. Both authors calculated life expectancy according to Lack's (1954) formula $E = (2-m)/2m$ (m = average adult mortality).

5.3 *Age composition*

Almost 60% of the population consists of birds from three, four or five years old. These findings are in agreement with the findings of Austin & Austin (1956) at Cape Cod, USA. They found an age composition which consisted of 17.7% three year old birds, 20% four year old birds and 15% five year old birds. DiCostanzo (1980) found a completely different age composition at Great Gull Island, USA. He found that over 70% of the birds were six year or older and over 50% were older than ten. This is in agreement with the high survival rate he found.

Ring wear and ring loss play only a role in the older age-classes. But even then ring loss causes no significant effect on our calculations of the age composition. However, the samples of the older age-classes are perhaps too small to detect a significant difference. In an age composition as found by DiCostanzo, ring loss and wear will play a more significant role. Furthermore, the assumptions used by Hatch & Nisbet (1983a) are probably inaccurate for rings used by the Dutch ringing scheme. They studied several rings carried by Common Terns in the USA. Their aluminium size 2 ring is the most likely to correspond with the rings used by the Dutch ringing scheme before stainless steel rings came into use in 1990. However, the size 2 rings have an internal diameter of 4 mm, while the rings used by the Dutch ringing scheme have an internal diameter of 4.2 mm. This causes differences in wear and loss of rings, which is greater in rings with larger internal diameter (Hatch & Nisbet 1983a).

Differences in height and thickness have also effect on ring wear and loss. Furthermore, the alloy of the rings used in the USA and the rings used in the Netherlands may have been different. Finally, differences in habitat also causes differences in wear and loss. Despite these differences, the estimates of Hatch & Nisbet are the only available estimates so far. Correcting for rings put on the tibia or the tarsus is not possible. However, Perdeck & Wassenaar (1981) found no significant difference between the wear of rings on tibia or tarsus in a 12 years study of the Black-headed Gull.

There are some records of immigrating birds. These birds are part of the Dutch population and should be taken into account. This can only be done accurately when the numbers of foreign birds are corrected for ringing effort in the country of origin. As this was impossible in the available time, no correction for ringing effort has been made. However, there are just a few immigrating birds recorded at the Euring Data Bank, so the effects of not taking them into account are assumed to be negligible.

5.4 *Age at first breeding*

One fourth of the population consists of new breeding birds. All birds probably breed at the age of four. Other authors assumed that all the birds breed at the age of five (Austin & Austin 1956, Nisbet 1978, DiCostanzo 1980). The majority of birds start breeding at the age of three. As Austin & Austin stated, it is possible that some birds do not breed for the first time until even later in life, and some adult terns may never breed at all.

5.5 *Survival until first breeding*

The survival until first breeding, found during this study, is very low. Ricklefs (1973) pointed out that the basic recruitment needed to maintain a stable population is equal to the adult mortality rate divided by the survival of young to breeding age. In this study, the basic recruitment should be 0.1324/0.035 = almost four young per bird = almost eight young per pair per year. This is not realistic. Mean clutchsize in most colonies varies between two and three eggs (Austin & Austin 1956, Glutz von Blotzheim & Bauer 1982, Cramp 1985, Geelhoed 1988, Becker 1991), so the population would collapse (there is hardly immigration; three or four birds (depending on the criteria) have been recorded at the Euring Data Bank). To some extent, there is exchange of colonies in the Delta area with colonies at Zeebrugge, Belgium, but this is more or less part of the Delta-area.

As already proposed, the survival rates estimated by the programme BROWNIE are not completely reliable for several reasons. Furthermore, the mean value used for fledging success from Griend amounts to 0.35. This is rather low and probably not representative as a mean value for the whole of the Netherlands. Fledging succes incorporates two stages: (1) hatching succes; (2) survival of young until fledging. Hatching succes has been calculated for the Delta-area by Geelhoed (1988) between 1986 and 1988 and amounts to 0.90. This is in agreement with the findings of Becker (1991) in several colonies in the German Waddensea-area. A (mean) value for the survival of young until fledging has never been calculated accurately in the Netherlands, although an important amount of the mortality occurs during this stage (Langham 1972). At this moment, there are no values for fledging succes in The Netherlands which are more realistic than the mean value of Griend. If the mean value for fledging success from other countries (see table 3 in Stienen & Brenninkmeijer 1992) is used, the weighed survival until first breeding amounts to 0.099. The basic recruitment should then be 13.24/9.9 = 1.34 young per bird = 2.67 young per pair. This value is still high, but more realistic.

5.6 *Age related dispersal*

The results in table 4.11 show that young birds exhibit more dispersal than adult birds. This is found for many species of birds (Greenwood 1980, Greenwood & Harvey 1982, Coulson & De Mévergnies 1992). Although the difference in dispersal direction is not significant, birds ringed as young seems to establish themselves in Southwestern direction, while birds ringed as adult seems to establish themselves in Northeastern direction. A similar phenomenon was found in the Kittiwake (Coulson & De Mévergnies 1992), but it is not easy to see what the biological backround may be. The lack of significance is perhaps the result of the small sample size.

5.7 *Separating the sexes*

Several authors have used biometric measurements to determine the sex of birds from which the sexes look alike (Anderson 1975, Thomas 1981, Green 1982, Piersma 1982, Coulson *et al.* 1983, Wood 1987, Green & Theobald 1988, Wood 1988). Frequently used characters are weight, bill-depth, bill-length, wing-length and total head-length (head plus bill). Weight changes with season. A study on Herring Gulls has shown that bill-depth increases with age (Coulson *et al.* 1981). Bill length is difficult to compare when data from more than one observer are involved, because it is hard to find the nasal-frontal hinge in a live bird. Wing-length is only a good measurement when the longest primaries are not moulting, growing or extremely abraded. Total head length has proven to be the most useful measurement (Thomas 1981, Coulson *et al.* 1983, Van Rhijn 1985, Barrett *et al.* 1989). Coulson *et al.* have shown that in three gull species the total head length was the single most accurate indicator of sex. Using more than one character did not lead to any improvement.

In order to use total head length for sexing Common Terns, two assumptions must be made: (1) The male is the larger sex, and (2) the total head length measurements are normally distributed within each sex (Coulson *et al.* 1983). In Common Terns, as in probably all Laridae, the male is the larger sex, but there is considerable overlap (see for example Harris & Hope Jones 1969, Coulter 1986, Cramp 1985, Glutz von Blotzheim & Bauer 1982). Assumption two is usually fulfilled for lineair measurements in birds.

The point of inflexion found during this study is not very strong. However, the discriminant value seems to be rather reliable, according to the 12 bird of known sex. So this measurement can be used in the field to separate the sexes of the Common Tern.

The total head length of the Common Tern is not recorded in the literature. Bill length, however, is given in many sources (Glutz von Blotzheim & Bauer 1982, Cramp 1985, Malling Olsen 1994). The bill length measurements from the literature will be used for indirect comparisons.

Both Cramp (1985) and Malling Olsen (1994) mention that the bill of males is longer than the bill of females. The percentage difference is 5.12 according to Cramp and 2.99 according to Malling Olsen. The percentage difference between the total head length measurements found during this study is situated between those percentages. According to Cramp, there is considerable overlap between the bill length of the sexes. According to Malling Olsen, the overlap is almost complete.

It would be interesting if a collection of birds was available of which the sex had been determined by internal examination and of which the length of total head could be measured. This would help in checking the proportion of birds correctly identified to sex by the probability method. Moreover, the use of discriminant analysis would be possible. It was tried to obtain measurements of birds of known sex by study of skins in the Zoölogical Museum in Amsterdam and the Natural History Museum in Leiden. Post-mortem changes in measurements of culmen to skull from both fresh and museum samples do not differ significantly (Herremans 1985). However, study skins are of no use because the nape is broken in skinning. This makes it impossible to take accurate measurements of the total head length. For a project in 1992 some bloodsamples of Common Terns in the Delta had been taken. Probably the sex of each bird had been determined in the course of this study. However, the results are not yet available (C.T. Murk, pers. comm.). The measurements of twelve dissected Common Terns from the Delta were available. These birds had been collected in 1989, for toxicological investigation by the RIKZ.

5.8 *Sex related dispersal*

In most species of birds both natal and breeding dispersal are more extensive among females (see for example Greenwood 1980, Greenwood & Harvey 1982, Bradly & Wooler 1991, Coulson & Mévergnies 1992). This seems not to be the case in the Common Tern. There is no significant difference in dispersal distance between males and females. The dispersal distance of males is even slightly larger than the distance of females. Perhaps the lack of difference between the sexes is caused by the dynamic nature of the colonies. Some colonies get destroyed by ground predators. Other colonies decline due to succession, for example colonies on newly created islands. The Common Terns of these colonies seek for other places to settle. They establish new colonies or settle in existing colonies. Both males and females are under inluence of this natural phenomenon, so both males and females exhibit clear dispersal.

Differences in dispersal direction between male and female seems to be more pronounced. In females, there seems to be no clear main dispersal direction. In males, the main direction seems to be southward. However, the difference between male and female is not significant. This is probably the result of the small sample size.

Note that not all the distances were calculated by the Euring Data Bank. Some distances were calculated in the course of this study, using the programme Circle. The author also calculated several dispersal directions. During a check, no differences with the Euring Data Bank results were found.

6 *Conclusions and recommendations*

This study showed that it is impossible to estimate the survival rate of the Common Tern accurately, because the survival rate differs between more than two years. An alternative survival rate, calculated and used during this study, amounts to 0.1977 ± 0.0257 for the first year of life after fledging and 0.8676 ± 0.0210 after the first year of life. The Dutch population consists for the majority of birds of three to five years old. Ring loss seemed to have little effect on the age composition, due to the relative large numbers of birds in younger age classes. Most birds start breeding during their third year of life. One fourth of the population consists of birds breeding for the first time. The weighed survival from egg until first breeding is estimated at 0.035, which is unrealistically low. This is caused by the use of the low estimates of fledging succes, taken from Griend. There are no better estimates of fledging succes in the Netherlands. Using an average estimate of fledging succes from other countries, the weighed survival until first breeding is 0.099. Young Common Terns exhibit more dispersal than adult birds, which is fairly common among birds. Young birds seems to disperse mainly in southwesterly direction, while adult birds disperse more to the northeast. Although the difference between the sexes of the Common Tern is not very strong, a discriminant value for total head length has been established and amounts to 78.1 mm. A small sample of twelve birds of known sex gives some confidence in this result. This value can be used in the field to sex birds. This method has been used to investigate differences in dispersal direction and -distance between the sexes. There is no difference in dispersal distance. This is probably due to the dynamic nature of colonies. Females exhibit no clear main dispersal direction. In males, the main dispersal direction seems to be southward.

It is difficult to calculate survival rates from ringing recoveries, simply because there are too few recoveries of birds ringed as adult. The use of both recoveries and recaptures can offer some relief, although there are also few recaptures of birds ringed as adult. Participants in ringing schemes should put more effort in the recapture and ringing of adult birds, instead of just ringing young birds. Furthermore, they should only use stainless steel rings.

7 *Acknowledgements*

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8 *Summary*

Some aspects of the population dynamics of the Common Tern in the Netherlands have been studied. It appeared to be impossible to attain accurate estimates of the survival rate. Alternative survival rates, calculated and used during this study, amounts to 0.1977 ± 0.0257 for birds in their first year of life after fledging and 0.8676 ± 0.0210 for birds after their first year of life. The majority of breeding birds are three to five years old. Ring loss has a minor effect on the calculation of the age composition. Most birds start breeding at the age of three. The weighed survival until first breeding amounts to 0.035, but is probably too low due to the availability of low estimates of fledging success. Young birds disperse over a greater distance than adult birds. In young birds, the main dispersal direction seems to be southwestward, in adult birds it seems to be northeastward. To separate the sexes in the field, a discriminant value for total head length is established at 78.1 mm. Between the sexes, there is no difference in dispersal distance. Although females seems to have no main dispersal direction, in males the main dispersal direction seems to be southward.

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