BIRD-BANDING

A JOURNAL OF ORNITHOLOGICAL INVESTIGATION

VOL. XXVII | APRIL, 1956 | NO. 2

SOME DEMOGRAPHIC ASPECTS OF THE CAPE COD POPULATION OF COMMON TERNS

(Sterna hirundo)[1]

BY OLIVER L. AUSTIN, M.D., AND OLIVER L. AUSTIN, JR.

The population of Common Terns that breeds each summer in the scattered terneries on Cape Cod and vicinity is undoubtedly the most thoroughly banded single bird population of any size in the world today. We have yet to develop an entirely satisfactory method of censusing it, but our estimates made over the past 30 years show it to range from about 15,000 to a maximum of perhaps 20,000 nesting adults, in company with about 4,000 *Sterna dougalli* and a few hundred *S. paradisaea.*

Ever since the late Edwin Howe Forbush banded the first few hundred chicks at Tern Island, Chatham, in 1923, an increasingly larger percentage of the annual crop of young has been banded every summer, at first on Tern Island alone and, since 1929, on all the other terneries occupied by the species in the region. The yearly totals of *hirundo* chicks banded within the Cape Cod group since 1925 have ranged from a low of 2,018 (1950) to a high of 17,786 (1953). The average annual chick yield over the years has been about 8,500, and the grand total of chicks banded from 1923 through 1955 is 254,614.

The first experimental work with adults by trapping incubating birds on their nests was started in 1929, when 863 adults were taken. As our skill in trapping developed, larger and larger samples were taken each breeding season. Since 1935 from 1,000 to 7,000 adults have been trapped every summer, yielding an annual sample of from 5 to perhaps 35 percent of the breeding population. In the 26 years of trapping (none was done in 1934) we have trapped a total of 112,512 adults, of which 41,754, or 37 percent, were returns. Study and analysis of these returns have been most rewarding; they have been the basis of most of the papers published on the terns by both senior and junior authors during the past 28 years.

Among the more interesting and important aspects of tern biology which study of the returns has clarified are: first, that very few terns nest during their second and third summers, and some not until their fifth summer; secondly that they tend overwhelmingly to return to breed at their natal site, and that this "site tenacity," as we have termed it, becomes stronger with age; thirdly that "group adherence," a tendency for individuals to remain together, plays a major role in

[1]Contribution Number 49 from the Austin Ornithological Research Station.

maintaining the population; fourthly that once mated, terns tend to stay mated to the same mates throughout their breeding life.

In several previous publications (see bibliography) we have given estimates, drawn from the data available at the time, of the tern population's probable age composition, mortality and survival, and on the species' possible longevity. Our calculations were limited by the figures at hand, which had and still contain a number of unavoidable variables and biases, and our conclusions, though presented as tentative, have been criticized, quite justifiably, for our failure to take all possible biases into consideration. We propose in this paper to re-examine the statistical evidence, which is now more complete and voluminous than ever, and to attempt to formulate a more accurate and reliable picture of some of the more important aspects of the demography of the Common Tern.

The most important biases affecting our return figures are first those caused by variations in the annual sampling effort, secondly by variations in the size of each cohort[1] banded, and thirdly by band loss. The first two are easily calculated and allowed for. Variations in the annual sampling tend to cancel out when a composite of a series of successive years is used in a time-specific table. Variations in cohort

[1]The term "cohort" is used to signify the group of terns hatched in any one particular year.

TABLE 1

Composite time-specific life table based on returns of Common Terns banded as chicks and trapped on nests, 1940 through 1955. Figures for lx are the 16-year averages of numbers of birds taken annually per 100,000 banded in each age class.

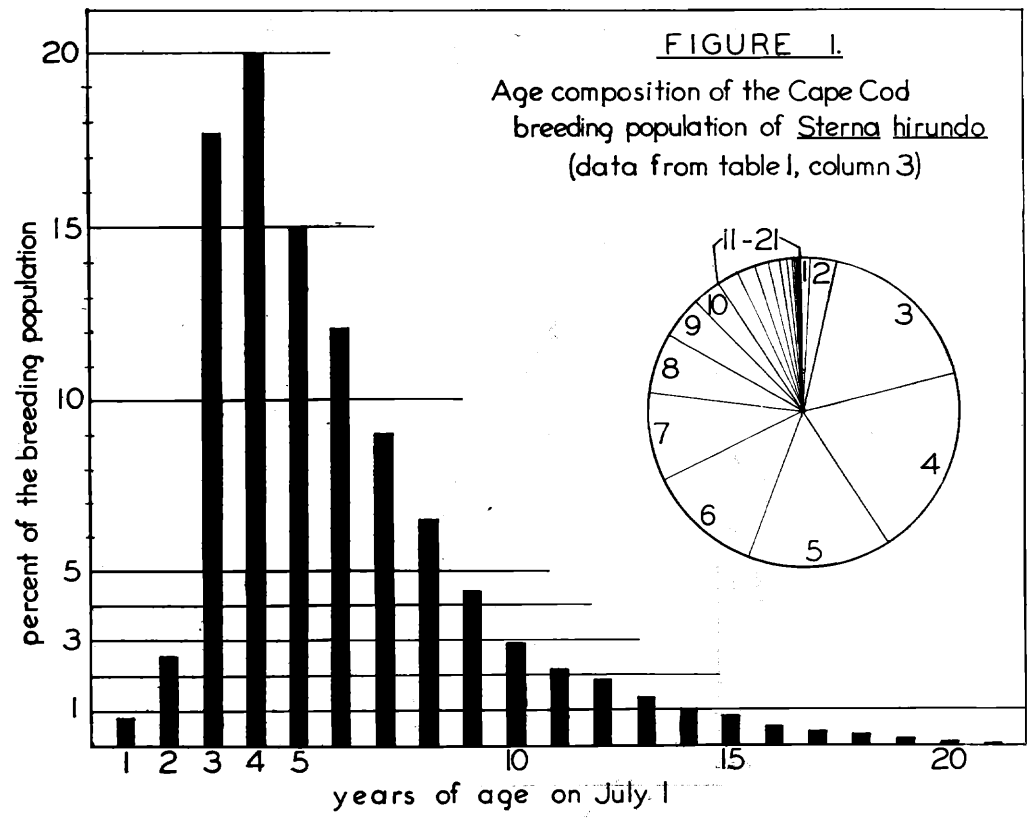
x Age interval in years	lx Alive at start (1 July)	Percent of population in each age group	dx Calculated deaths each year	qx Mortality rate per year
1-2	41.7	0.8		
2-3	140.4	2.6		
3-4	937.4	17.7		
4-5	1058.6	20.0	263.0	25.0%
5-6	795.6	15.0	152.2	19.3
6-7	643.4	12.1	168.9	26.3
7-8	474.5	9.0	129.3	27.3
8-9	345.2	6.5	111.8	32.4
9-10	233.4	4.4	82.4	35.3
10-11	151.0	2.9	33.5	22.2
11-12	117.5	2.2	18.0	15.3
12-13	99.5	1.9	24.8	24.9
13-14	74.7	1.4	21.1	28.3
14-15	53.6	1.0	8.3	15.5
15-16	45.3	0.86	15.7	34.7
16-17	29.6	0.56	7.2	24.3
17-18	22.4	0.42	5.1	22.7
18-19	17.3	0.33	7.9	45.6
19-20	9.4	0.18	5.1	54.4
20-21	4.3	0.08	3.8	88.5
21-22	0.5	0.01	0.5	100.00

Mean annual mortalities: 4 through 22 years = 25.3%
4 through 18 years = 25.0%

size can be eliminated by expressing the numbers of each cohort captured in any later year as percents of the totals of that cohort originally banded. Bias from band loss, however, is more difficult to estimate.

We have never been able to arrive at a satisfactory estimate of band life. While the government bands are all made to fairly rigid specifications, experience has shown that almost no two series resist abrasion and corrosion equally. Some series of bands we have found worn thin and almost undecipherable in 5 or 6 years; a few have remained strong and readable after being worn 20 years. Band wear likewise varies with the individual tern — the band on a bird nesting in loose, open sand obviously is subjected to much more abrasion than is one on a tern that habitually nests in grass. A fair average for the older series is somewhere between 8 and 12 years. We have great hopes for the new series we have used since 1950, which have been treated electrolytically to make them more resistant to corrosion by salt water.

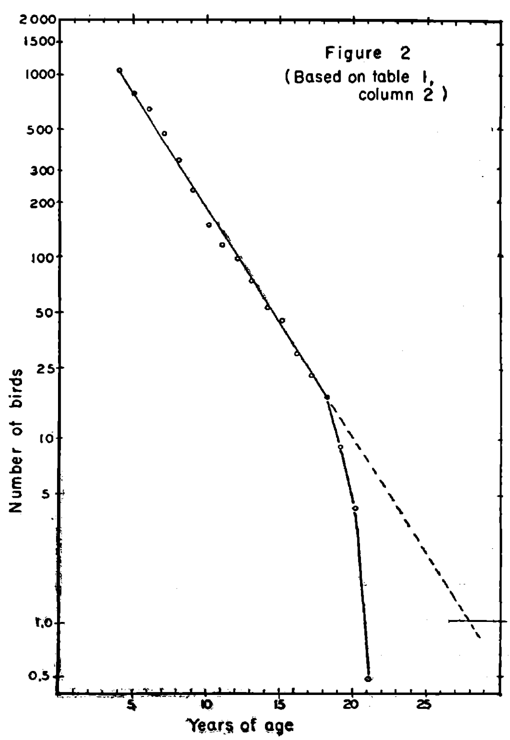
We have tried our best to overcome band loss since we first noted obvious wear in the bands in the first adults we trapped in 1929. Our practice at first was to replace any band that appeared worn or thin, but we soon found it easier just to add a second band to the bird's



other leg. Since 1940 our practice has been to add a new band to every bird we find wearing a band it has carried 8 or more years. Some rebanded birds in our population are now wearing their third bands. This policy has been gratifyingly effective, and in our more recent figures bias from band loss is seldom apparent, except in the very oldest birds, and somewhat questionable even there. That it is still a factor to be reckoned with, however, is evident in the fact that our annual sample of adults remains in the neighborhood of 37 percent banded — despite our banding at least 90 percent of each year's crop of young, and a fifth or more of the adults each year. The only other explanation is a constant and sizable influx of birds from other terneries, which the extremely low percentage of foreign-banded birds among our returns shows does not occur.

Age Composition of the Population

The most reliable, unbiased, and revealing series of figures available from our return records are those presented in table 1. These are derived from the 6,965 adult terns banded as chicks (so their ages are known accurately), trapped since 1940 on nests in the Cape Cod group. Returns taken previous to 1940 have been eliminated, because up to that time no cohort of the banded population was more than 15 years of age, and including them slants the percentages unequally toward



the younger segments. The banded sample has been more than adequate for all ages since then. A composite of the 16 years of trapping eliminates minor sampling variables, and expressing the numbers of each age group taken as percents of the number of that group banded eliminates bias from the varying sizes of each banded cohort.

Column 2 of figure 1 shows the numbers, per 100,000 banded, captured in an average year from 1940 through 1955. Column 3 gives the relative incidence of each age-group in the population, and is the basis for the bar-graph and pie-graph shown in figure 1. These show at a glance the relative importance of each age group to the maintenance of the population. Less than 1 percent of the breeding population nests in its second summer, and only 2.6 percent in its third. Three-year-old birds, starting their fourth summer, comprise 17.7 percent of the breeding colony, and 4-year-olds 20 percent.

The pie-graph shows the productive backbone of our population to be birds from 3 to 10 years old, in their 4th to 11th summers; these comprise 90 percent of the breeding population. Birds less than 3 years of age comprise only 3.4 percent of the breeding colony, birds over 10 years old less than 7 percent. The importance of this small segment of older birds in the population is apparently far greater than its size suggests. These are the birds in which site tenacity and group adherence are most firmly established, and they are largely reponsible for keeping the group together as a unit and returning it to the same place year after year.

The comparatively long breeding life of the terns, most effective from the 3d through the 10th years, is most important to maintaining a population with a comparatively low rate of reproduction—the species rears but one brood each year, and lays, with few exceptions, a maximum of 3 eggs per clutch; the average appears to be about 2.3 eggs per clutch (Austin 1932:126). Some years production is almost nil in one or more of the colonies, as a result of accidents and disease. Such disasters would be fatal to a short-lived species such as the Mourning Dove, which matures more rapidly, is much shorter-lived, and is heavily dependent on each year's crop of young to maintain the breeding stock (Austin, Jr., 1952). In the terns the effects of a year of low production do not show in the breeding population until the 3d year following, and may be remedied completely before the 4th year by the coming to breeding age of a large cohort produced the following year.

Adult Mortality

Table 1 also gives us our best estimate of adult mortality and survival. We assume of course that all birds breed by their 5th summer, and continue to nest annually from then until they die. While it is possible that some birds do not breed for the first time until even later in life, and some terns may never breed at all, we have no evidence of it. The regular slope of the curve in figure 1 from year 4, when all birds are breeding, to year 21, which is as far as our data go, shows that its parameters are well established. We can judge the rate of change of this annual mortality best by plotting the figures in column 2 of table 1 on semilogarithmic paper, as in figure 2. This shows how remarkably steady the adult mortality rate remains from the 4th through the 18th year. We can offer no better proof of the validity of the apparent mean annual mortality of 25 percent in the adult terns from their 4th through their 18th years.

Of particular interest are the points beyond the 18th year. Here our sample is indeed small, 14 birds out of 100,000, represented in any one year by only 2 or 3 terns in our population of 15-20,000. But note that the curve continues downward, showing a steady increase in a mortality that has remained a straight line the previous 14 years. Were these last three points more scattered we might question their validity, but their regularity suggests they reflect truthfully what is occurring in our population. Our continuous rebanding of all older birds handled during the past 25 years reduces the possibility that this sudden increase in the disappearance rate is caused by band loss. As we have been unable to demonstrate the presence of nonbreeding birds in the terneries, or of very old birds on the wintering grounds during the breeding season, we believe the figures to be valid evidence of an increasing death rate incident to the onset of old age in the 19th year.

LONGEVITY

What then do these figures show us about longevity in the Common Tern? We have already seen that the segment of the population 18

TABLE 2

Dynamic Life Table of Common Terns banded as chicks in 1934, based on known survivals (returns and recoveries) through 1955.

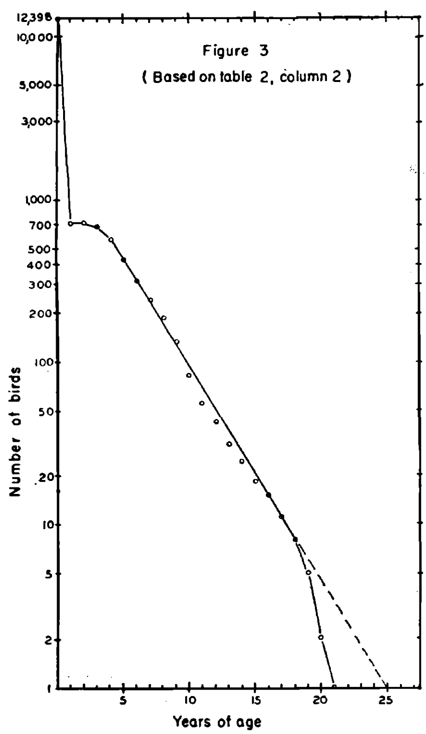
x Age interval in years	lx Alive at start (1 July)	dx Calculated deaths each year	qx Mortality rate per year
0-1	12,398	11,698	94.5%
1-2	700	7	1.0
2-3	693	27	3.9
3-4	666	102	15.3
4-5	564	148	26.2
5-6	416	108	25.9
6-7	308	69	22.6
7-8	239	55	23.0
8-9	184	52	23.0
9-10	132	49	37.1
10-11	83	28	33.8
11-12	55	13	23.6
12-13	42	11	26.2
13-14	31	7	22.5
14-15	24	6	25.0
15-16	18	3	16.7
16-17	15	4	26.6
17-18	11	3	27.3
18-19	8	3	37.5
19-20	5	3	60.0
20-21	2	1	50.0
21-22	1	1	100.0

Mean annual mortalities: 0 through 4 years = 81.8%
4 through 22 years = 26.3%
4 through 18 years = 26.1%

and more years of age is remarkably small. By projecting the 25 percent mortality rate beyond the 18th year, we see that a population of 100,000 birds will have dwindled to an ineffective single bird at the 28th year.

Heretofore we have assumed that this was the probable ultimate life-span of the species, but the chances seem against it. Only time and continued banding and trapping will tell, but consider that we have taken only a single bird banded as a chick that has reached the age of 21. The first potential 21-year-old banded birds reached that age in 1944. By 1955, the original banded sample of birds 20 + years old, that is birds banded as chicks previous to 1936, was 71,129. By the laws of chance we should have trapped by this time at least 10 or more 20-year-olds instead of the 6 we have, 4 or 5 instead of a single 21-year bird, and certainly a few even older.

The oldest Common Tern in our records we banded as a nesting adult of unknown age in 1929. When we found it freshly owl-killed at Tern Island, Chatham 23 years later in 1952, it must have been at least 24 years old. This record, the 26-year-old Caspian Tern banded and recovered in Michigan, and the Arctic Tern banded and found dead in Germany at the age of 27 (Bergstrom 1952:72) show a few individuals can and do reach such advanced ages. But for all practical purposes we can consider the maximum productive life span of the Common Tern to be about 20 years.



DYNAMIC CORROBORATION

It is of interest to check the adult mortality rate of 25 percent obtained from the composite time-specific sample of our population with that shown by the dynamic analysis of a single cohort. Our largest and most adequate single set of figures is for the cohort of 1934, an extremely successful and productive year during which we banded 12,398 Common Tern chicks. The subsequent history of this cohort is shown in table 2. Column 2 shows the number of birds we know to have been alive each successive year, and column 4 the annual estimated mortality each year. The curve (figure 3) is not as smooth as that for the combined time-specific sample, but it duplicates its essential features remarkably closely. The slight increase in the mean annual mortality from the 4th through the 18th years is from failure to capture all surviving birds — but considering that we take less than one-third of the birds present each year, the bias is remarkably small. This error has of course been reduced by consistent, consecutive trapping, and by assuming birds taken for the first time in the later years to be alive in all earlier years.

One other set of figures is of interest, those showing the history of a group of 1,000 adults trapped and banded consecutively in the heart of the Tern Island colony between May 19 and May 30, 1936. These birds were of unknown age when banded, and their ages as shown in table 3 as starting with x years. Of interest here is the high first year disappearance, which reflects an obvious bias, unquestionably from failure to recapture all survivors. The means here are most significant. That of the 28.6 percent from year x + 1 to through year x + 6 is the soundest, and its increase of 3 percent over that shown by the large

TABLE 3

Dynamic life table based on known survival of 1,000 Common Terns banded as adults on Tern Island in 1936 (series 35-317,000 thru 35-318,000).

Year	x	lx	dx	qx
1936	x to x + 1	1,000	468	46.8%
1937	x + 1 to x + 2	532	145	27.3
1938	x + 2 to x + 3	387	118	30.5
1939	x + 3 to x + 4	269	82	30.5
1940	x + 4 to x + 5	187	52	27.8
1941	x + 5 to x + 6	135	33	24.4
1942	x + 6 to x + 7	102	43	42.1
1943	x + 7 to x + 8	59	26	44.1
1944	x + 8 to x + 9	33	13	39.4
1945	x + 9 to x + 10	20	7	35.0
1946	x + 10 to x + 11	13	7	53.8
1947	x + 11 to x + 12	6	3	50.0
1948	x + 12 to x + 13	3	0	0.0
1949	x + 13 to x + 14	3	1	33.3
1950	x + 14 to x + 15	2	0	0.0
1951	x + 15 to x + 16	2	1	50.0
1952	x + 16 to x + 17	1	0	0.0
1953	x + 17 to x + 18	1	1	100.0

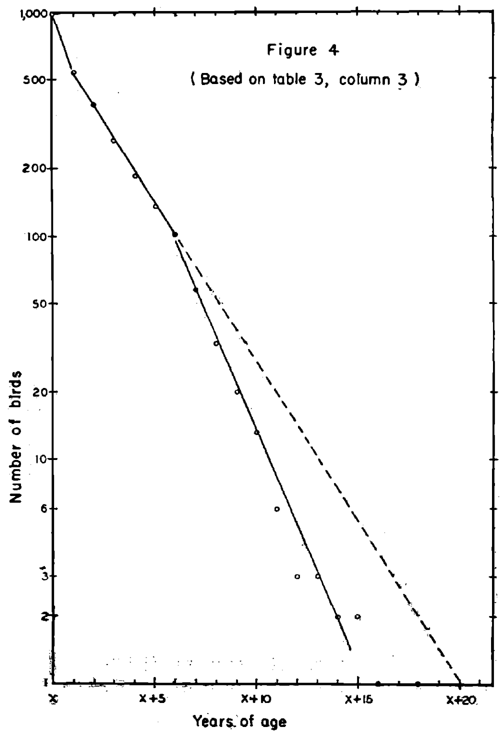
Mean annual mortalities: x through x + 17 years = 36.3%
x + 1 through x + 6 years = 28.6%
x + 6 through x + 17 years = 41.7%

time-specific sample of chick-banded adults is again the result of inadequate later sampling, inevitable in a dynamic analysis.

The sharp break after the 6th year, shown graphically in figure 4, where the rate increases to 41.7 percent, is understandable only when interpreted in the known history of the colony. In 1942 the section of Tern Island in which this group nested began to disintegrate, and the birds moved elsewhere, a few to other parts of Tern Island, most of them to other terneries — North Point, Bird Island, Ram Island, Plymouth, etc., where they were not as well sampled. Inadequate sampling is quite obvious in the irregular distribution of the points from the 11th through the 18th years.

Early Mortality

Because the Common Tern does not return to breed in quantity until its 4th summer, our return figures do not indicate the mortality during the first 4 years. Indeed, we have no way of figuring this early mortality that is not subject to considerable bias. Table 2, based on the 1934 cohort of chicks in a dynamic analysis, shows the first year mortality to be 94.5 percent. The total returns and recoveries received to date from all chicks banded up through 1950 is only 4 percent, giving a composite first-year mortality of 96 percent over the years.



Were this valid, our population of terns, whose maximum possible reproductive potential is 3 young per pair per year, would long ago have become extinct. The figure is obviously badly biased, partly perhaps by band loss, but primarily by inadequate sampling. As we have no way of estimating accurately the magnitude of either of these influences, no satisfactory way exists of deducing from the return figures a reasonable estimate of the early mortality.

The only banding figures of significance in this regard are those of birds banded as chicks and reported as recovered dead by the general public. These may be compiled into a composite dynamic life table and analyzed by what is now commonly known as Lack's method. The method has worked well with a number of other species, but is somewhat disappointing in the terns, mainly because so few recoveries are obtained after the first few years of life.

From our tremendous sample of 180,207 chicks banded from 1923 through 1950 we have received to date (1955) the ridiculous total of 500 usable recoveries, only 0.28 percent of the total banded. Space does not allow comment on why we should receive only one-tenth the number of recoveries from tern banding in this country that similar but much smaller tern banding programs in Europe receive. We consider the inscription on the bands largely to blame — the instructions for reporting on the size 3's seem too cryptic for finders to comprehend.

The recovery figures analyzed by Lack's method are shown in table 4. The bias in the later years from inadequate sampling is immediately apparent. The 76.8 percent first year mortality seems reasonable, but coupled with a 2nd year mortality of 50.8 percent and a 3rd year of 43.9 percent is manifestly impossible. At this rate fewer than 5 percent of each cohort produced would survive to breeding age, and to replace

TABLE 4

Composite dynamic life table of Common Terns, based on *recoveries* of birds banded as chicks through 1950, received to 1955.

x Age interval in years	lx Alive at start	dx Number of recoveries	qx Mortality rate
0-1	500	384	76.8%
1-2	116	59	50.8
2-3	57	25	43.9
3-4	32	10	31.2
4-5	22	9	40.9
5-6	13	6	46.1
6-7	7	3	42.9
7-8	4	1	
8-9	3	0	
9-10	3	1	
10-11	2	0	
11-12	2	1	
12-13	1	0	
13-14	1	1	

Mean annual mortalities: 0 through 14 years = 65.5%
0 through 3 years = 70.0%
3 through 14 years = 35.5%

the annual mortality of 25 percent in the breeding population, each pair of terns would have to rear 9 or 10 young each year.

In exploring the probable magnitude of the elusive early mortalities, we may estimate the survival necessary to maintain the population in the light of the species' reproductive potential. We have unfortunately not been able to measure the Cape Cod population's reproductive success as accurately as we would like for this purpose, but a reasonable estimate of it from our observations over the years is 1 for 1, or 2 young per pair fledged to banding age per season. At this rate if the population is to remain stable, we can see from column 3 of table 1 that an average of 20 percent of each year's group of young must survive to breed at the age of 4 years.

First year mortality has been demonstrated conclusively to be much higher than adult mortality in all species — the reasons why are too obvious to need comment. With a total mortality of 80 percent allowable during the first 3 years of life, however, the first year mortality alone cannot be this great unless no birds are to die in the 2nd and 3rd years. As birds do die in this period, the probable first year mortality must be somewhat lower than 80 percent, just how much lower depending on the death rate during the succeeding 2 years. Once the critical first year is passed and the young have learned by experience how to avoid the deadly pitfalls of youth, their mortality is certainly no higher than the 25 percent demonstrated for the breeding population. With 2nd and 3rd year mortalities of 25 percent, the first year mortality cannot be above 53 percent in a stable tern population.

As terns are more vulnerable to their enemies while nesting than at any other time in their life cycle, it is extremely likely that the mortality in the nonbreeding "subadults" 1, 2, and 3 years old is considerably lower than in the breeding population. To the best of our knowledge this group remains throughout the breeding season on the wintering grounds where hazards are fewer and survival chances higher. If the mortality in this group of birds is 10 percent per year, a tern population fledging 2 young per pair can withstand a first year mortality of 72 percent; with a 15 percent annual mortality in the nonbreeding young adults, the maximum first year mortality allowable is 67.5 percent.

If the species' reproductive success is higher, it can withstand even higher early mortalities. Assuming a productivity of 2.2 young per pair for instance, a 20 percent mortality in the nonbreeding adults allows a first year mortality of 65 percent. In good breeding years our population's productivity may well be this high or higher, thus providing the surplus necessary to fill the gaps left by such recurrent disastrous years as 1950, when instead of the anticipated 15,000, we found only 2,068 chicks to band.

SUMMARY

The reproductive backbone of the Cape Cod population of Common Terns is composed of birds from 3 to 10 years old. These comprise 90 percent of the breeding population. Birds less than 3 years old comprise only 3.4 percent of the breeding colonies, birds more than 10 years old less than 7 percent.

Though individuals do attain greater ages, the maximum reproductive life-span of the Common Tern appears to be about 20 years.

The mean annual mortality of the breeding population is constant at 25 percent from the 4th through the 18th years. The steady increase in the annual mortality rate after the 18th year suggests the onset of old age in the 19th year.

If the population is to maintain itself, at least 20 percent of the young fledged to banding age must survive to breed at the age of 4 years. The first year mortality appears to be between 60 and 70 percent. The 2nd and 3rd year mortalities are probably considerably lower than the 25 percent shown by the breeding population.

LITERATURE CITED

AUSTIN, O. L., SR., M.D.

1940 Some Aspects of Individual Distribution in the Cape Cod Tern Colonies. *Bird-Banding,* **11**: 155-169.

1942 The Life Span of the Common Tern. *Bird-Banding,* **13**: 150-176.

1945 The Role of Longevity in Successful Breeding by the Common Tern. *Bird-Banding,* **16**: 21-28.

1947 A Study of the Mating of the Common Tern. *Bird-Banding,* **18**: 1-16.

1949 Site Tenacity, A Behavior Trait of the Common Tern. *Bird-Banding,* **20**: 1-39.

1951 Group Adherence in the Common Tern. *Bird-Banding,* **22**: 1-10.

1953 The Migration of the Common Tern *(Sterna hirundo)* in the Western Hemisphere. *Bird-Banding,* **24**: 39-55.

AUSTIN, O. L., JR.

1951 The Mourning Dove on Cape Cod. *Bird-Banding,* **22**: 149-179.

BERGSTROM, E. ALEXANDER

Extreme Old Age in Terns. *Bird-Banding,* **23**: 72.

North Eastham, Cape Cod, Mass.