POPULATION DYNAMICS OF A COMMON TERN COLONY

By Joseph DiCostanzo

This paper presents the results of a preliminary study of the population dynamics of a colony of Common Terns (*Sterna hirundo*) on Great Gull Island, Suffolk Co., New York, based on analysis of data from 12 years of trapping and banding at the island.

The earliest intensive banding study of the Common Tern was that of the Austins on Cape Cod, Mass., starting in the 1920's (Austin, Jr., 1929, 1932; Austin, Sr., 1942, 1949, 1951; Austin and Austin, 1956; and others). More recently, Grosskopf (1964) in Germany and Nisbet (1978) on Cape Cod have estimated mortality rates and other population parameters. Possibly due to differences in sampling methods and sample sizes, these studies all arrived at higher adult mortality rates than I found in this study.

The colony on Great Gull Island has been the subject of a study of the breeding biology of the Common Tern since 1966 (Cooper et al., 1970; Hays, 1970). Part of this study has been an intensive banding program of both young and adult birds in the colony. From 1966 to 1978, 15,677 young and 6,768 adult terns were banded with U.S. Fish and Wildlife Service (USFWS) aluminum bands. In 1977 and 1978, more than 60% of the breeding adults in the colony were trapped. Of these, 79% in 1977 and 87% in 1978 were previously marked individuals. Of trapped adults, 26% in 1977 and 30% in 1978 were of known age (i.e., originally banded in their hatching year). I have used the results of the 1977 and 1978 seasons, combined with other data from the last 12 years, to determine adult mortality rate and survival of fledglings to breeding age. I have also briefly examined the movements of adults and young between Great Gull Island and other colonies.

STUDY AREA AND METHODS

Great Gull Island, 17 acres in area, lies at the eastern end of Long Island Sound, in Suffolk County, N.Y. Historically the site contains a mixed colony of Common and Roseate terns (*S. dougallii*); the birds abandoned the island at the turn of the century when the government built a fort there (Heilbrun, 1970). The army left in 1949 and the terns began to nest again in 1955. From 1966 to 1968, researchers visited the island on weekends to mark nests and band, occasionally staying for a week or two during the nesting season. The current program was initiated in 1969 and since then researchers have arrived at the island late in April or early in May every year and have remained on the island until early September.

As part of a nesting success and productivity study (Hays and Risebrough, 1972), a team checks the island daily and marks nests with numbered wooden tongue depressors. Newly hatched young are banded with a numbered, colored plastic band. When the chicks are at least

| Тав | le 1 | |
|-----|------|--|
| | | |

| | 1977 | 1978 |
|---|-------|-------|
| Banded birds of unknown age | 1,439 | 1,589 |
| Banded birds of known age | 722 | 842 |
| Previously unbanded birds | 587 | 361 |
| Total birds handled | 2,748 | 2,792 |
| Estimate of breeding birds ¹ | 4,434 | 4,250 |

Common Terns trapped on Great Gull Island in 1977 and 1978.

¹ Based on corrected nest count. See text.

a week old, the plastic band is removed and is replaced with a standard, butt-end, size 2 USFWS aluminum band and a combination of colored plastic bands.

The team also traps adult terns by placing treadle traps over hatching eggs or newly hatched chicks. Trapping is done twice a day, between 0600 and 0800 and again between 1800 and 2000. An effort is made to capture both members of a pair. This trapping program is carried out daily, except during rain or heavy fog, from the time the first eggs hatch in early June until the last eggs hatch in late July or early August.

After an adult is captured it is banded with a unique color combination, identifiable in the field, consisting of three plastic colored bands and a USFWS aluminum band (Hays, 1970). If the bird is banded when trapped, the age and condition of the bands are checked. Worn or thin aluminum bands are removed and the bird is rebanded. After seven years all aluminum bands are removed, regardless of condition, and the bird is rebanded. In addition, all bands originally placed on nestlings are removed and the first time it is trapped as an adult.

Among the difficulties in studying population dynamics of the Common Tern is the staggered way in which young birds enter the breeding population. Although a few nest when one or two years old and probably a majority at age three, a sizeable percentage wait until age four (Austin and Austin, 1956). It is almost impossible to census or even adequately sample these young nonbreeders, some of which remain on the wintering grounds (Austin, 1953). Therefore, throughout this paper I have used age four as the date of initial breeding.

Table 1 includes estimates of the number of birds nesting in the Great Gull Island colony in 1977 and 1978, based on ground counts of the nests marked throughout the season, with a correction for renests.

The number of renests was determined by examining the nesting history of birds trapped during the latter part of the season. It was necessary to examine groups of nests, initiated at successively later times in the season, because the percentage of renests increases during the course of the season as birds try again after an unsuccessful first attempt. For convenience, I grouped nests based on their tongue-depressor numbers, i.e., 1901–2000, 2001–2100, etc. These groups actually contained <100 nests each because the Roseate Tern nests on the island are included in the same numbering system.

In each group I separated the nests into five categories based on our nesting histories of the birds trapped on the nest. Category I contained known renests, nests where the birds had been trapped earlier in the season. In category II were probable renests, nests with birds that had a history of nesting earlier in the season in previous years. Comparisons between years were made by comparing the date of hatching of a bird's first egg relative to the date of the first hatched egg of the season. A bird was considered to be a probable renester if it was approximately 10 or more days later than it had been in previous years. This is the approximate minimum interval that birds on Great Gull Island have needed to renest after an unsuccessful nesting attempt (Hays, pers. comm.). Category III contained nests with birds that had a history of nesting at the same time or later in previous years. Category IV included nests with two- to five-year-old birds without known nesting histories. Most birds of these ages tend to nest late (Hays, 1978). Finally, category V contained nests with previously unbanded birds; very few of these were found because the colony has such a high percentage of banded birds.

I assumed that the nests in categories I and II were all renesting attempts and that the nests in categories III, IV and V were all first nesting attempts. For those nests where both members of the pair had been trapped, the nest was counted only once and it made no difference to which category it was assigned if both birds indicated the nest was either a renest or a first attempt. In cases where a conflict occurred I assigned the nest to the probable renests because this gave a more conservative figure for the total number of nests in the season. Finally, I assumed that the trapped sample in each group of nests was representative, and that the proportion of first nesting attempts vs. renesting attempts was the same in both the trapped and untrapped nests.

To avoid checking every trapped nest in both years I used the first known renest, as found by trapping, as a starting point and checked the groups of nests through the end of the season. I also checked the groups of nests prior to this for probable renests, as defined above. I checked back until I found no probable renests in the trapped samples, back to approximately nest 1500 in 1977 and 1200 in 1978. Prior to this is the peak period of egg laying at the beginning of the season, a period of 10 to 14 days in both years. It is unlikely that there was time for many, if any, renests during this period. The trapping coverage in the groups checked was similar in the two years, an average of 55% and 54% of the nests had at least one bird trapped in 1977 and 1978, respectively.

Possibly the number of renests may have been underestimated, because some of the unknowns may have been renesters, but because such a high percentage of the birds in the colony are banded and have doc-

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umented nesting histories, this bias is thought to be small. It is also possible that the proportion of nests with young parents may have been underestimated. Because nests are trapped at hatching and young parents possibly have a lower hatching success, a pattern that Coulson and Horobin (1976) found in Arctic Terns (*S. paradisaea*), nests with young parents might have failed prior to hatching and thus might have been underrepresented in the trapped sample. This would tend to make the figure for renests too high. Thus the estimates of breeding birds might be somewhat conservative. Any other bias in this method should have been similar for both 1977 and 1978 and thus should have the same effects on any calculations for both these years using these estimates.

I subtracted the number of renests found by the above method from the total nests marked to give a corrected number of nests for the season. The uncorrected totals were 2,839 and 2,777 marked nests for 1977 and 1978, respectively. Subtracting the renests, the corrected totals are 2,217 and 2,125, respectively. The colony has been stable at approximately 2,100 to 2,200 pairs for at least the last 12 years. Previously published population estimates for this colony did not have a correction figured for renests (Duffy, 1977, Appendix Table 1).

The total number of birds handled in 1978 in Table 1 includes 122 incubating birds identified by sight by their color combinations and not trapped. These birds tend to be concentrated towards the early part of the season during the peak of nesting. Most of these birds were of unknown age and their inclusion in the totals does not significantly change the calculated results.

Hays (1978) has shown that the 6- and 7-year-old birds tend to nest earlier, with a hatching peak in early June, and that 4- and 5-year-old birds nest successively later in the season. In 1976, a week of rain in early June prevented us from trapping during the early part of the hatching peak. For this reason, in the analysis that follows, the trapping data in 1976 were not used to calculate mortality even though nearly 50% of the colony was trapped that season.

RESULTS

The annual adult mortality was determined in two different ways, using two different types of life-table approaches. In the first method I calculated the number of banded birds alive in several different hatching-year classes, or cohorts, in the colony in 1977 and 1978. These figures, analogous to time-specific life tables as defined by Hickey (1952), were then compared to determine the mortality between the two years for each cohort. The results are given in Table 2. The second and third columns list the numbers of birds from each cohort trapped in each season. The calculated figure for the size of each cohort (columns four and five) was obtained by multiplying the number trapped by the total number of birds in the colony divided by the total number of birds trapped (Davis, 1951). The difference between 1977 and 1978 in the numbers calculated for each cohort is presumably attributable to mor1970

1971

1972

1973

| Aortality of adul in | | | oirds banded as sting there in 1 | | |
|-------------------------|------|------------------|----------------------------------|---------------------|---------|
| Hatching | | ber of rapped | | calculated blony | Percent |
| year | 1977 | 1978 | 1977 | 1978 | loss |
| 1969 | 115 | 114 | 186 | 174 | 6.5 |

140

169

232

103

128

158

212

93

| | | TABLE 2. | | | |
|------------------|-------------|----------|-----------|--------------|---------|
| f adult Common ' | Terns based | on birds | banded as | nestlings on | Great (|

84

104

139

61

87

105

144

64

tality. These differences, expressed as percent loss, are given in the last column. Because the comparisons being made are for the same cohort between one year to the next and not between two different cohorts, it is not necessary that the banded samples be the same size in the original hatching years.

In the second method individual cohorts were followed over a span of years and a survivorship listing made of total individuals known to have been alive at each year of age. This type of listing of survival data is a dynamic life table (Hickey, 1952). Table 3 gives such survival listings for the 1969, 1970, and 1971 cohorts, based on all recoveries made through the 1978 nesting season. Only these three cohorts have been used because only these had had sufficient time for recoveries to accumulate. Obviously any bird reaching a given age must have been alive in previous years. Continued trapping in upcoming years will undoubtedly recover birds that have been missed for one or more years and hence will reduce the mortality shown in Table 3. Therefore these figures should be considered as maximum mortality only. Because of the large percentage of the colony trapped in recent years, nearly 50% in 1976 and over 60% in 1977 and 1978, it is unlikely that the mortality rates in Table 3 will be lowered by more than a few percentage points. The mean annual mortality from Table 2 is 8.0% (SD = 1.4) and the mean maximum mortality from Table 3 is 9.2% (SD = 1.9).

Table 4 gives the minimum and calculated survival to age four of fledglings from six cohorts that have returned to nest on Great Gull Island. The minimum survival is based on the total recoveries on the island through 1978, of birds from these cohorts at age four or older $(\bar{x} = 11.9)$. The older cohorts have been subject to recovery in more years than the younger ones, so their minimum survival is closer to the calculated figure. The calculated survivals are projections based on the trapping data for 1977 and 1978. The figure for the 1973 cohort was taken directly from the calculated number in Table 2 for 1977. Using the same formula as described above in the calculations for Table 2, the

8.6

6.5

8.6

9.7

| | | 69 ng year | | 70 ng year | | 171 ng year |
|-----|----------------|-----------------|----------------|-----------------|----------------|----------------|
| Age | Known alive | Percent loss | Known alive | Percent loss | Known alive | Percen loss |
| 4 | 237 | _ | 167 | _ | 198 | _ |
| 5 | 224 | 5.5 | 152 | 9.0 | 176 | 11.1 |
| 6 | 203 | 9.4 | 137 | 9.9 | 156 | 11.4 |
| 7 | 182 | 10.3 | 124 | 9.5 | _ | — |
| 8 | 169 | 7.1 | _ | _ | _ | _ |

TABLE 3.

Mortality of adult Common Terns based on birds banded as nestlings on Great Gull Island in 1969 through 1971 and known to be alive¹ in later years.

¹ Includes birds recovered off Great Gull Island.

1974 cohort survival was figured from 156 birds trapped in 1978. For the other cohorts the 8% annual mortality rate previously determined was used to project backwards to age four from their calculated size in 1977 (Table 2). The survival thus calculated ranges from 10.4 to 16.7% with a mean of 14.3% (SD = 2.6).

The percentage of fledged young surviving and returning to breed at Great Gull Island may in fact be slightly higher than shown. The figures used here for the original sizes of the banded cohorts are the total number of young banded at one week of age or older and not found dead in the colony thereafter. These figures are somewhat higher than the true fledging figures; almost all chick mortality occurs in the first week to 10 days after hatching, but some occurs between that age and fledging (Langham, 1972; Nisbet and Drury, 1972).

Recoveries of Great Gull Island young at other colonies show that not all surviving young return to the island to nest. These recoveries indicate that at least an additional 1 to 2%, and probably more, of fledglings survive but nest in other colonies as adults. When these recoveries are taken into consideration the known minimum survival ranges from a low of 10.9% for the 1973 cohort to a high of 19.5% for the 1972 cohort ($\bar{x} = 14.2\%$).

Few data are available so far on the extent of intercolony movements of adult terns. Austin (1949) found that having once nested, terns tend to return to that same site year after year. He also found that many birds moved to a different colony to renest if their first nest failed, but that these birds also tended to return to the first site in subsequent years. This shifting on renesting complicates the problem of measuring intercolony movements of adults, because a bird trapped in the latter half of a breeding season may not be at its home colony. Birds may, in fact, move considerable distances when they renest; twice in the last 12 years birds trapped on nests on Great Gull Island early in the season have 1974

1.424

| Hatching | Young | Min | limum | Calc | ulated |
|----------|--------|-----|---------|------|---------|
| year | banded | n | Percent | n | Percent |
| 1969 | 1,562 | 221 | 14.1 | 260 | 16.6 |
| 1970 | 1,399 | 149 | 10.7 | 180 | 12.7 |
| 1971 | 1,519 | 176 | 11.6 | 200 | 13.2 |
| 1972 | 1,588 | 236 | 14.9 | 252 | 15.9 |
| 1973 | 991 | 91 | 9.2 | 103 | 10.4 |

| TABLE 4. |
|--|
| Survival of Common Terns to age four, based on birds banded as nestlings on Great Gull |
| Island and recovered there in later years. |

been trapped later the same season incubating eggs on Cape Cod, Mass., approximately 120 miles to the northeast.

10.9

237

156

A trapping program at a colony near Great Gull Island suggests, perhaps, the extent of the real movements of breeding adults. Falkner's Island lies off the Connecticut shore in Long Island Sound approximately 28 miles west of Great Gull Island. The colony on Falkner's Island has recently greatly increased in size, more than doubling since 1975, to 1,300 to 1,500 pairs of Common Terns in 1978. With this rapid growth the colony might reasonably be expected to have picked up many Great Gull Island adults if they had been shifting about.

In 1978, Fred Sibley and Jeffrey Spendelow of Yale University, in cooperation with the Great Gull Island Project, trapped 1,474 nesting adults on Falkner's Island. Of these, 148 had been banded as nesting adults on Great Gull Island either in that year or in previous years; $4\tilde{6}$ of these had been trapped earlier in that season on nests on Great Gull Island. Of the remaining 102 birds, 40 were trapped on Falkner's Island in the latter half of the season, after 30 June; some of these 40 may also have been renesters from Great Gull Island. Of the remaining 62 birds, 34 were originally banded on Great Gull Island as late season nesters; some of these may have been renesters from other colonies. This leaves only 28 birds that apparently definitely shifted colonies. Applying the same type of ratio as used earlier, approximately half the Falkner's Island colony was trapped in 1978, so this equals approximately 56 Great Gull Island adults in the colony there. These birds were from 12 breeding seasons, 1966 to 1977, during which approximately 5,000 adults were banded on Great Gull Island before 1 July. Fifty-six birds would thus represent 1.1% from all seasons combined. A number of colonies closer than Falkner's Island might be expected to contain a higher percentage of birds from Great Gull Island but they are all fairly small, most being approximately 100 pairs or less (Duffy, 1977) and so do not involve many birds.

Possibly some adults may return to a colony after breeding in another for a year or two. A pair of hybrid Common \times Roseate terns (Hays,

16.7

| Hatching | | No. | Trapp Great Gi | |
|----------|-------------------------|---------------------|-------------------|---------------|
| year | Location | banded ¹ | 1977 | 1978 |
| 1970 | Jones Beach Cape Cod | 1,702 1,045 | | |
| 1971 | Jones Beach Cape Cod | 1,793 1,472 | -3 | $\frac{1}{2}$ |
| 1972 | Jones Beach Cape Cod | 1,817 1,294 | $\frac{1}{2}$ | 1 3 |

| TABLE 5. |
|---|
| Common Terns hatched on Jones Beach and on Cape Cod and trapped on Great Gull Island in 1977 and 1978. |

¹ Data from Gochfeld (1975) and Nisbet (1978).

1975) found nesting on Great Gull Island in 1972 and 1973 were trapped on a nest on Cape Cod in early June 1974. In early June 1976, this pair was again found nesting on Great Gull Island. This may not have been typical behavior for a normal pair of Common Terns.

Finally, there are the movements of young birds. As with adult movements the data so far are limited, but do give an indication of the area over which interchange of young birds occurs. Birds hatched and banded on Great Gull Island have been found as breeders in nearly every colony in eastern Long Island Sound where trapping has been done. They have been found in colonies from Cape Cod to Jones Beach on the south shore of western Long Island, N.Y., approximately 80 miles southwest of Great Gull Island. In 1978, Hans Blokpoel of the Canadian Wildlife Service trapped two birds from Great Gull Island, aged two and six, at a colony in Toronto harbor, Lake Ontario.

Birds have been trapped on Great Gull Island that were hatched at colonies along the east coast as far south as Cape May, N.J., and as far north as Sugarloaf Island, off Popham Beach, Me., as well as one bird from Ontario, Canada. Most recoveries have been from colonies within 40 miles of the island, but we regularly recover birds from Jones Beach and from Cape Cod.

Surprisingly, the limited data so far available seem to indicate a higher influx from Cape Cod than from Jones Beach, even though Cape Cod is one and a half times farther away. Table 5 lists the number of young banded on Jones Beach and Cape Cod in 1970, 1971, and 1972 and the number of birds from each of these cohorts trapped on Great Gull Island in 1977 and 1978. The numbers trapped are small, but in each case the pattern is the same: more Cape Cod birds are trapped despite more birds having been banded on Jones Beach. Data were not available on the number of young banded at these two locations in 1969 and 1973 but no Jones Beach birds were trapped on Great Gull Island from either of these years in 1977 or 1978. One bird hatched on Cape Cod in 1969 was trapped on Great Gull Island in 1977 and in 1978, and one bird hatched on Cape Cod in 1973 was trapped on Great Gull Island in 1977.

DISCUSSION

Farner (1955) stressed the importance of testing results such as these by comparing them with the known productivity of a species. An examination of the results presented in this paper shows them to be reasonable in comparison with known productivity. 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. The mean adult mortality rate, 8.0% (from Table 2), divided by the mean survival to age four, 14.3% (from Table 4), gives a figure of 0.56 young per bird, or 1.1 young per pair per year needed to maintain the colony. In an analysis of data from Great Gull Island from the 1976 field season, Hays (1978) found that productivity increased with the age of the parent to 1.0 and 0.8 young per pair for the 6- and 7-year-olds respectively, the oldest age groups available for study at that time. The difference in productivity between these two age groups was not statistically significant with the sample sizes available. Grosskopf (1964), Gochfeld and Ford (1973), Nisbet (1973), and Langham (1974), studying colonies in Germany, New York, Massachusetts, and England, respectively, all report productivities in the range of 0.8 to 1.2 young per pair. Thus, the productivity here calculated to be needed to maintain the Great Gull Island colony is within the known range of productivity of the species and is close to the known productivity of the colony.

From the above, the Great Gull Island colony appears to be producing young at a rate a little below that necessary to maintain itself. Because the colony has been stable for a number of years the difference is presumably made up by immigration. But if the adult mortality were lower or the survival to breeding age higher, then the required productivity would be lower and the colony might be capable of maintaining itself without immigration. The recovery of young hatched at Great Gull Island and breeding at other colonies shows that the survival to breeding age is higher than that indicated when only birds returning to the island are used to calculate survival. It is therefore possible that the colony is capable of maintaining itself without immigration, but that some low level of intercolony exchange of young birds is normal and probably beneficial to a colony. Such exchange would prevent reproductive isolation and inbreeding of individual colonies.

The 8% annual adult mortality presented here for the Common Tern is considerably lower than the 25% of Austin and Austin (1956), the 19% of Grosskopf (1964), and the 17% of Nisbet (1978). One possible reason why the Austins' study, the most extensive banding study of the species to date, arrived at such a high mortality figure could be that they combined results from several colonies. The Austins trapped at colonies all over Cape Cod; many of the colonies were small, unsuccessful, and relatively unstable, shifting about from year to year (Austin, 1942). This instability would tend to lower recovery rates because the birds were moving about to such a large extent and perhaps even moving in and out of the study area. Lower recovery rates would raise the apparent mortality. Nisbet (1978), in a reexamination of the Austins' data, correctly inferred an annual adult mortality of 9% for the years of their study. This was based on an assumed juvenile survival of 8% from fledging to age four. This rate of juvenile survival is considerably lower than the average minimum of survival of 14.2% known for Great Gull Island young, based on all recoveries.

Nisbet (1978), in his own study, also combined data from several colonies on Cape Cod. In addition, his mortality figure was calculated indirectly from an estimate of the number of 4-year-olds entering the population. This estimate was based on a relatively small sample of 83 banded birds, of which only 19 were 4-year-olds, out of a total sample of over 1,500 birds trapped from a population estimated at 10,000. Finally, the Cape Cod population, the subject of both the Austins' and Nisbet's studies, has been steadily declining since the 1920's (Nisbet, 1973) and perhaps does not have population parameters typical of a stable population.

Grosskopf's (1964) mortality rate of 19% would require an unusually large juvenile survival rate, approximately 38% to age four, to maintain the population based on its productivity of one young per pair. Juvenile birds tend to have a much lower rate of survival than adults (Lack, 1946). Even if the juveniles reached the adult survival rate as early as their second year, the 19% annual mortality would require 72% survival of fledglings at the end of their first year to achieve a 38% survival at age four. This is only a little lower than adult survival.

The relatively low productivity and delayed maturity of the Common Tern is typical of seabirds in general. The low adult mortality found for the Great Gull Island colony is also typical of the mortality rates found for other seabirds that have been studied. Ashmole (1971) summarized the annual adult mortality rates for 17 species of seabirds studied by that time. Eleven had annual rates of 10% or less. The remaining six ranged up to a high of 19% for the Common Tern, a rate taken from Grosskopf (1964). In searching the literature I found 20 additional species for which mortality rates have been published since Ashmole's review, as well as revised figures for several species previously studied. Most mortality rates for the new species as well as the revised figures were low. Table 6 presents mortality rates for 10 members of the Stercorariidae and Laridae published since Ashmole's review. Five of the species have rates <10%.

The mortality rate found in this study can be used to estimate average life expectancy. From the formula (2 - m)/2m (Lack, 1954), where m represents annual adult mortality, the average expectancy of further

| Species | Mortality (%) | Reference |
|--------------------------|------------------|-----------------------------|
| Catharacta skua | 7 | Furness (1978) |
| C. macormicki | 6 | Carrick and Ingham (1970) |
| | 6.2 | Wood (1971) |
| Stercorarius parasiticus | 20 | O'Donald and Davis (1975) |
| S. longicaudus | 9-16 | Andersson (1976) |
| Larus delawarensis | 13 | Ludwig (1974) |
| L. argentatus | 6.5 | Chabrzyk and Coulson (1976) |
| L. novaehollandiae | under 10 | Carrick (1972) |
| Rissa tridactyla | ♀ 14 | Coulson and Wooler (1976) |
| - | ð 19 | |
| Creagrus furcatus | $1.2-6.5^{1}$ | Harris (1979) |
| Sterna paradisaea | 12-13 | Coulson and Horobin (1976) |

TABLE 6.

| Average annual adult mortality for the Stercorariidae and Laridae. |
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¹ Not annual mortality, but based on nine-month period between breeding seasons.

life for a Common Tern reaching age 4 is 12 years. This assumes that adult mortality is independent of age at least through age 16. Botkin and Miller (1974) have recently questioned the theory of age-independent mortality in birds, contending that the low mortality found in seabirds would result in potential longevities >100 yr for individuals of some species. However, the formula they use to calculate the potential longevity from annual mortality rates does not take into account that fractions of an individual are not possible; populations must be in whole numbers. This consideration makes little difference in the calculated potential longevities of birds with high annual mortalities, but becomes increasingly important with lower annual mortalities. Botkin and Miller calculate that, with annual mortalities of 6% and 3%, it would take 102 and 228 yr, respectively, to reduce a population of 1,000 to one individual. However, because partial individuals are allowed, the formula requires 52 and 105 yr, respectively, to reduce the last 25 individuals to one, with the given annual mortalities. Botkin and Miller also fail to consider the possibility of an age-independent mortality for most of a bird's life span with senescence causing sharply higher mortality in the oldest age classes.

In the Great Gull Island colony the mortality and survival rates indicate that approximately 8% of the birds are four years old and approximately 7% are five. Because a number of birds breed at age three, but very few at a younger age, some percentage of the colony, probably under 8%, are birds three years old or younger. Therefore, over 70% are six years old or older and over 50% are 10 or older.

Apart from their numerical superiority, the importance of the older age classes to the colony is enhanced by the low productivity of the younger birds. It is not until the birds are six years old that they begin to reproduce at a rate high enough to maintain the colony; the older birds are also the first to start nesting (Hays, 1978). Thus, it is the older birds that are the important nucleus of the colony, in terms of both maintenance of the colony and of initiation of nesting. The importance of the older birds to the success of a colony was first suggested by Austin (1945), but for different reasons, and he assumed a much shorter life span for individual birds.

The delayed maturity and staggered entrance of young Common Terns into the breeding population, as well as the relatively low level of productivity needed to maintain a stable population as a result of the low adult mortality, have important implications for the species. The effects on the breeding population of low productivity in a poor nesting season are small and are delayed for three or four years. By that time possibly the effects are partially or even completely offset by a number of other factors.

Table 4 shows a considerable variation in the survival of young from different years. The reasons for this variation are not yet known, but an increase in the percentage of young surviving, if it occurred in that same year, might partially make up for a low number of young fledged. Weather conditions and predation made the 1968 nesting season an extremely poor one on Great Gull Island (LeCroy and Collins, 1972), but the 1968 cohort has had one of the highest rates of survival and return of any year of the study. Nearly 17% of the 172 fledglings banded that year have been recovered as breeding adults.

Also, because an entire hatching-year class does not enter the breeding population in a single year, a small cohort could be augmented by birds from the hatching years both before and after it. These bracketing hatching years may have been ones of high productivity.

Finally, Farner (1955) pointed out that adult mortality can be expected to fluctuate from year to year. Increased survival of adults, perhaps as a result of lowered competition on the wintering grounds from a smaller number of juveniles, would lower the number of new breeders needed to maintain the population.

All these factors mean that the species can easily tolerate occasional, or even several consecutive nesting seasons of lowered productivity. Only a sustained decline in productivity, or a sustained increase in mortality of adults or young, would be potentially serious. The effects of these would also be gradual in their appearance, especially those resulting from lowered productivity, because the low mortality and consequent longevity of adults would slow the decline. If senescence is a factor, the population might appear to be declining only gradually, but would then drop sharply as large portions of the population reached old age.

Finally another possibility, given the population parameters found in this paper, is that one or a few very productive colonies might be able to maintain a population that appears to consist of many colonies. Because of the low recruitment necessary to maintain itself, a highly successful colony would produce many excess young that would be available to maintain marginal colonies nearby. Thus, maintenance of a population might be dependent on one or a few colonies and hence be vulnerable to a reduction in the success of these few successful colonies.

SUMMARY

Trapping and banding data from an intensively studied Common Tern colony are analyzed to determine population parameters for the colony, and their significance is discussed. Adults have an annual mortality rate of approximately 8%. An average of 14.3% of the fledged young return to nest at the colony as adults. At least an additional one to two percent survive, but nest in other colonies. Intercolony exchange of adults and young is briefly examined. Adult exchange is thought to be low. The results of this study are shown to be reasonable in relation to the known productivity of the colony and the species.

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Due to an unexpected, yet welcome, recent influx of new members into NEBBA, the usual reserve supply of the Winter 1980 issue (Volume 51, No. 1) of *Journal of Field Ornithology* has been exhausted. To supply future requests for complete sets and for other new members, we badly need any unwanted copies of this issue. If anyone can donate a copy to NEBBA, please send it soon to the Treasurer, ELISSA LANDRE, 278 Eliot Street, South Natick, MA 01760. Such a donation would be greatly appreciated and is, of course, tax deductible.

NEW EDITOR

With a great deal of pleasure, the NEBBA Council announces the appointment of a new Editor for Journal of Field Ornithology. He is DR. JEROME A. JACKSON, Department of Biological Sciences, Box GY, Mississippi State University, Mississippi State, MS 39762. Dr. Jackson brings to the position considerable scientific and editorial experience, especially as Editor of the Wilson Bulletin for several years. Effective immediately, all new manuscripts, revisions of old ones, and all correspondence dealing with editorial matters should be addressed to Dr. Jackson.

As an epilogue, may I express my sincerest appreciation to NEBBA Council and officers, past and present, and to the scores of reviewers and authors with whom I have dealt over the past nine years. Special recognition should also be given to Recent Literature editors—Jack Hailman, Bert Murrary, and Jed Burtt. Through mutual cooperation, diligence, and sacrifice, we have effectively combined efforts to produce a journal of high scientific quality, one of national and international stature.—DAVID W. JOHNSTON.