POPULATION MODELS FOR COMMON TERNS IN MASSACHUSETTS

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The population of Common Terns (Sterna hirundo) breeding in Massachusetts has been declining for at least 30 years (Nisbet, 1973). The decline appears to have accelerated in recent years: although at least 9,000 pairs were known in 1970, only about 7,700 pairs were found in a comprehensive survey in 1972 (ibid.), and only 5,100–5,300 pairs in similar surveys in 1975 and 1976 (Table 1). Although the counts suggest the possibility of a slight recovery in 1976, the average rate of decrease in the breeding population between 1970 and 1976 was 8–10 percent per annum, in contrast to an average rate of only 3–4 percent in the period 1952–1970 (Nisbet, 1973).

In an attempt to determine whether the recent decline has been due to a failure of recruitment of young birds into the breeding population, I made an intensive search in 1975 for breeding adults banded as chicks in earlier years. Although the numerical estimates of recruitment obtained thereby are quite rough, they seem sufficient to justify comparison with earlier data from the same regional population, and to support conclusions about the reason for the accelerated decline.

My survey in 1975 was designed to estimate the proportion of birds aged 4 and 5 years in the regional breeding population. Although many Common Terns breed at the age of 3, some do not (Austin, 1942; Austin and Austin, 1956); my data indicate that those doing so are generally unsuccessful in raising young and that they usually nest late in the season, too late for inclusion in population surveys conducted in the first half of June. Most Common Terns breed at the age of 4 (Austin and Austin, 1956); accordingly the proportion of 4-year-olds is the best measure of recruitment into the effective breeding population. The proportion of 5-year-olds gives an independent measure of recruitment (after allowing for intervening mortality). I have not used data on birds aged 6 or older because (a) precise data are lacking on the number of young Common Terns raised in Massachusetts prior to 1970, and (b) the likelihood of band-loss is substantial by the age of 6.

METHODS

Between 6 and 18 June, 1975, two assistants and I searched for banded terns in 25 plots in three colonies. The colonies chosen—Bird Island (41°40′N, 70°43′W), Yarmouth (41°43′N, 70°15′W) and Monomoy (41°38′N, 69°58′W)—included about two thirds of the Common Terns breeding in Massachusetts in 1975 (Table 1). At each site a blind was set up overlooking a relatively open patch in the colony. Between 30 and 50 nests were marked with numbered stakes and watched for about two hours; banded and unbanded birds were recorded as they walked on and off their nests. In most cases at least one bird could be checked at each nest, and at many nests both birds were checked during incu-

Table 1
Estimated numbers of Common Tern pairs nesting in Massachussetts.¹

Colony	1970	1972	1975	1976
Ram Is., Mattapoisett	300	220	0	0
Bird Is., Marion	250	310	400	470
Nashawena Is., Gosnold	100	35	20	45
Nomans Land, Chilmark	1,200	1,000	$(100)^2$	180
Martha's Vineyard (3 colonies)	$n.d.^3$	160	100	90
Craigville Beach	n.d.	90	75	50
West Dennis Beach	50	75	120	40
Sampson's Is., Cotuit	n.d.	40	30	75
Monomoy Is., Chatham	3,950	1,750	2,250	2,350
Tern Is., Chatham	750	425	6	0
Nauset New Is., Eastham	0	130	250	450
Jeremy's Point, Wellfleet	0	20	140	0
Gray's Beach, Yarmouth	900	1,450	700	900
Plymouth Beach	1,500	1,450	550	400
Snake Is./Castle Is. (Boston Harbor)	n.d.	275	180	180
Tinker's Is., Manchester	n.d.	50	n.d.	40
Plum Is., Newburyport	50	100	90	20
Other small colonies	2	140	84	52
Known total of pairs	9,050	7,720	5,100	5,370
Known total of breeding adults	18,100	15,440	10,200	10,740

¹ Data from Nisbet (1973) and censuses in 1975 and 1976.

bation change-overs. After each watch the banded birds were trapped and their bands were removed for study of band-wear. Altogether 1,536 birds (15 percent of the total population) were examined; of these, 83 were banded, 47 of them as chicks in Massachusetts.

The surveys were timed to coincide with the hatching of the earliest clutches in each colony and therefore included birds that had laid up to 22–24 days later than the earliest layers. Most 4-year-olds proved to have laid in the latter part of this period; 5-year-olds also were slightly later than average. Two banded birds that were still courting at the time of the surveys were later caught on eggs and proved to be 3 years old. Three banded birds that were discovered nesting still later proved to be 3, 2, and 2 years old. Thus it seems likely that the surveys were late enough to locate most or all of the birds 4 years old or older, but not late enough to locate all the birds 3 years old.

² Count made too late in the season (21 July) for reliable estimate.

³ n.d., no data.

Table 2

Common Terns banded as chicks in Massachusetts between 1970 and 1972 and found breeding there in 1975.

Year of hatching	Estimated breeding population (adults)	Estimated no. of young fledged	No. of young banded	No. found breeding in 1975
1972	15,400	3,400	1,294	11
1971	$17,000^{1}$	7,700	1,472	19
1970	18,100	8,500	1,045	9

¹ Estimated from data in Nisbet (1973).

RECRUITMENT

Table 2 lists the number of banded birds 3, 4, and 5 years old found breeding in 1975 and compares them with the numbers of chicks banded and estimates of the numbers of chicks raised in Massachusetts in the corresponding years. Estimates of the breeding population and average breeding success have been published previously (Nisbet and Drury, 1972; Nisbet, 1972, 1973), but the figure for breeding success in 1972 has been amended upwards slightly to incorporate information acquired subsequently.

The figures in Table 2 can be used to derive rough estimates of the total number of birds in each year-class breeding in 1975. Using 1971 as an illustration, 1,472 chicks were banded. Assuming that about 80 percent of these survived to fledging (a figure based on my own studies), about 1,180 banded chicks would have fledged; i.e., about 15 percent (1,180/7,700) of the fledglings were banded. Assuming that the 1,536 adults examined in 1975 were a representative sample of the entire population of about 10,200 breeding adults, the 19 banded 4-year-olds in the sample would correspond to $19 \times 10,200/1,536$ or 127 banded 4-year-olds in the entire population. Since about 15 percent of this yearclass had been banded, 127 banded birds would correspond to 127/0.15 or 850 4-year-olds in the entire population. A similar calculation for the 1970 year-class indicates that there would have been roughly 610 5-year-olds in the 1975 breeding population. (Assuming 17 percent annual mortality (see below), this year-class would have numbered about 740 in 1974, when its members were 4 years old.) For the 1972 yearclass the corresponding estimate is 240, but as noted above this is likely to underestimate the number of birds alive in 1975, because some 3-year-olds nested too late to be found in the survey and others probably did not nest.

Taken at face value, the data for the 1971 and 1970 year-classes suggest that about 10 percent of the chicks fledged in Massachusetts survived to enter the effective breeding population at the age of 4 years;

the corresponding annual recruitment rate would be about 7.5 percent (800 4-year-old recruits in a population of 10–11,000).

The most questionable assumption used in deriving the above figures is that the birds examined in 1975 were a statistically representative sample of those marked in 1970-72. Substantial numbers of Common Tern chicks were banded in each of the eight largest colonies in Massachusetts during 1970–72, and birds raised in seven of these colonies were recovered at Bird Island, at Monomoy, or at Yarmouth in 1975. However, the mixing of chicks raised in these colonies was incomplete: 26 of the 47 chicks retrapped in 1975 were breeding in the colony where they had been raised. Since no chicks were banded at Monomoy in 1970 and comparatively few were banded there in 1971, the sampling at Monomoy in 1975 likely underestimated the number of recruits there. However, this bias is offset by an opposite bias at Bird Island, where disproportionately large numbers of chicks had been banded in 1970–72. To estimate the net effect of these biases, I divided the Massachusetts population into three regional groups and calculated estimates of recruitment for each by the method outlined above. However, the overall estimate of recruitment obtained in this way was virtually identical with that obtained by aggregating the entire population. Thus, although both the banding in 1970-72 and the sampling in 1975 were biased, the biases apparently offset each other.

Among other potential sources of error in these estimates, the largest are probably in the estimates of average breeding success used in Table 2, which were derived by extrapolating from fairly small samples (Nisbet and Drury, 1972). Errors are also likely in the estimates of total population (Nisbet, 1973) and in the figure of 80 percent used above for the survival of banded birds to fledging. Because of these potential errors, the estimates of recruitment should be regarded as no more than semi-quantitative. However, after reviewing the sources of error I believe that the recruitment rate is unlikely to lie outside the range 5–10 percent.

IMMIGRATION

In addition to the 47 chicks banded in Massachusetts, the birds trapped in 1975 included 21 that had been banded as chicks on Long Island, New York. Table 3 relates the numbers of these immigrants 3–6 years old to the numbers of chicks banded on Long Island in the corresponding years. Assuming again that the birds examined in 1975 were representative of the entire Massachusetts breeding population, the finding of about 3 banded birds from each year-class suggests that about 20 banded birds raised on Long Island had entered the Massachusetts population each year. About 12,000 pairs of Common Terns nest on Long Island (Nisbet, 1973; Buckley et al., 1975, 1976). Assuming that their average productivity in the years concerned was about one fledged chick per pair (Gochfeld and Ford, 1973; LeCroy and LeCroy, 1974) and that 80 percent of the banded birds survived to fledging (Cooper et al., 1970;

Table 3

Common Terns banded as chicks on Long Island, New York, between 1969 and 1972 and found breeding in Massachusetts in 1975.

Year of banding	No. of chicks banded on Long Island	No. found breeding in Massachusetts in 1975	Age-class in 1975
1972	5,314	6	3 years
1971	5,042	2	4 years
1970	5,347	2	5 years
1969	4,651	3	6 years

LeCroy and LeCroy, 1974; Gochfeld, pers. comm.), the 5,000 chicks banded on Long Island each year (Table 3) would correspond to roughly one third of the number fledged there. Hence the 20 banded birds would correspond to a total of roughly 60 birds from Long Island entering the Massachusetts population each year, i.e., an immigration rate of roughly 0.6 percent.

The birds trapped in Massachusetts in 1975 included three others that had been banded as adults on Great Gull Island, Long Island, in 1973, 1972, and 1966. Because large numbers of breeding adults are banded each year on Long Island, especially at Great Gull Island (Cooper et al., 1970; H. Hays, pers. comm.; data supplied by the Bird Banding Laboratory), the finding of these three birds probably does not reflect significant immigration of breeding adults from Long Island into Massachusetts. An upper limit for such immigration would be 0.2 percent of the Massachusetts population per year.

So far little evidence exists for substantial emigration in the reverse direction. Although trapping of adults at Great Gull Island started in 1966 (Cooper et al., 1970), only one chick banded by O. L. Austin in Massachusetts has been recovered there (ibid., Table 1; Austin, Ms), despite the fact that Austin banded most of the chicks raised in Massachusetts through 1957 (Austin and Austin, 1956; Austin, Ms). Of 5,380 Common Terns banded as chicks in Massachusetts between 1968 and 1972 (probably 10-15 percent of the total number fledged in those years), only six had been found breeding at Great Gull Island through 1976. Because of the intensive program of trapping breeding adults at Great Gull Island, it seems unlikely that many others would have been missed. Although precise numerical comparisons are not possible, these data suggest that immigration into the Massachusetts colonies from Great Gull Island considerably exceeds emigration thereto. Although the breeding population on Long Island has been maintained or has slightly increased while that in Massachusetts has declined (Nisbet, 1973; Buckley et al., 1975, 1976), the data thus suggest net immigration into Massachusetts from Long Island.

Table 4

Tentative population models for Common Terns in Massachusetts in the periods 1940–56 and 1970–75.

	1940–56 (Austin and Austin 1956; Nisbet 1973; this paper)	1970–75 (this paper)	
Average no. of young raised per pair	1.1	0.9	
Survival of young to age 4	6–10%	7–13%	
Annual recruitment rate	4-6.5%	5-10%	
Net annual immigration rate	0	0-1%	
Annual decrease in population	3.5 – 4.5%	8-10%	
Annual adult mortality (inferred)	7.5–11%	13-21%	

A TENTATIVE POPULATION MODEL

Combining the estimates of 5–10 percent for average annual recruitment of locally-raised birds, 0–1 percent for average net annual immigration, and 8–10 percent for average annual decrease in breeding population, we can estimate the average annual loss of birds from the breeding population as 13–21 percent (Table 4). Unless substantial numbers of adult birds have not been breeding in recent years, this estimate of annual losses of adults must represent mortality. These estimates of recruitment and mortality depend primarily on returns of banded birds 4–5 years old: if there were significant losses of bands within 4–5 years, both estimates would be too low. However, preliminary studies of band-wear suggest that band-loss does not become significant before the age of 5 (Hatch and Nisbet, in prep.).

Similar estimates for the Massachusetts population of Common Terns in the period 1940–56 can be derived from the data of Austin and Austin (1956). They found that only 4.0–5.0 percent of Common Terns banded as chicks were subsequently retrapped as breeders (ibid., Table 2 and Austin, 1942:63–64). These figures are an incomplete measure of recruitment, because on the average only about 30 percent of the breeders were trapped each year (Austin and Austin, 1956: 55, 58). On the most conservative assumption, the average bird that survived to the age of 4 might have bred only twice before dying or losing its band: its chances of being retrapped would then have been only about 50 percent. It is more likely that the average bird would have bred three or four times while retaining its band: its chances of being retrapped would then have been about 66–76 percent. Hence the Austins' data suggest that 6–10 percent of birds banded as chicks survived to enter the breeding population.

To estimate the corresponding recruitment rate, the average breeding success in this period appears to have been around 1.1 fledged young per pair (Nisbet, 1973: Table 5), and the Massachusetts population was

then declining at an average rate of about 4 percent per year (ibid., p 37). Hence 1,000 adults in a typical year, X, would have produced about 550 fledged young; assuming 6–10 percent survival to age 4, these would have yielded 33–55 recruits in year X + 4; related to a breeding population of about 850 adults in year X + 4 these would have represented 4–6.5 percent recruitment. Net immigration at this period is believed to have been small or zero (Austin, 1951). Hence, combining the estimate of 4–6.5 percent annual recruitment with that of 3.5–4.5 percent annual decrease, we can estimate the average annual mortality of adults as 7.5–11 percent (Table 4).

Austin and Austin (1956) themselves estimated the average annual mortality of adults as 25–29 percent, based on life-tables constructed from returns of birds banded as chicks (ibid., Tables 1 and 2, Figs. 2 and 3) and as adults (ibid., Table 3 and Fig. 4). However, their life-table based on returns of chicks required that almost 65 percent of the breeding population consisted of birds only 3–6 years old (ibid., Fig. 1): this is manifestly incompatible with the observed return rate of only 4.0 percent for birds banded as chicks, which as shown above places an upper limit of 9–10 percent on the annual recruitment of 4-year-olds. Another major inconsistency is in their life-table based on returns of adults (ibid., Table 3): 47 percent of the birds trapped as adults were never trapped again, although the rate of disappearance after the first retrapping amounted to only 29 percent annually. Both these anomalies suggest major biases against trapping of birds already banded.

One recognized source of bias is band-loss. Austin and Austin (1956: 57) reported rebanding most birds trapped with bands over 8 years old, but in fact many may have lost their bands earlier. As they pointed out (p. 58), "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." This anomaly suggests that more than one half of the birds must have lost their bands before being retrapped.

Another likely source of bias is "trap-shyness." Austin sampled breeding Common Terns by placing traps over nests with eggs, moving the traps to other nests if no birds were caught within a short period. However, I have observed that banded Common Terns are often extremely reluctant to enter traps: this would result in substantial bias against banded birds in the trapped sample. The anomalously high rate of disappearance of adults after the first trapping (Austin and Austin, 1956, Table 3) suggests that a substantial number of their Common Terns were permanently trap-shy.

Each of these biases would lead to substantial underestimation of the return rate, and hence to overestimation of adult mortality. Accordingly, I would reject Austin and Austin's estimates of annual mortality as subject to serious biases, and place greater weight on the population model derived from returns of chicks and from overall population trends (Table 4).

CONCLUSIONS

Comparing the population models derived for the periods 1940–56 and 1970–75 (Table 4), no evidence exists for a substantial change in the rate of recruitment to the breeding population. Nor is there evidence for a substantial decline in net immigration. Hence the recent acceleration in the rate of decline of this population appears to be due to an increase in the adult mortality rate, from roughly 9 percent to roughly 17 percent per annum. This conclusion can be drawn despite the uncertainty in both estimates of recruitment rates: it depends mainly on the observed increase in the rate of decline.

The apparent marked increase in adult mortality rate has ominous implications for conservation (Nisbet, 1976). Adult mortality during the breeding season appears to be very low: the number of adults found dead in the breeding colonies is usually much less than 1 percent of the total population. Hence most mortality probably takes place during migration or on the winter quarters where protection will be difficult. At present, recruitment of new birds to the breeding population appears to fall short of adult mortality by a factor of 2–3 (Table 4): local programs to protect breeding birds cannot close this gap, although they can prevent its widening (Nisbet, 1976).

SUMMARY

Fifteen percent of the Common Terns breeding in Massachusetts were examined in 1975; 83 banded birds were located and trapped. Data from birds banded as chicks in 1970 and 1971 suggest that the survival rate between fledging and the age of 4 was 7–13 percent, and that 4-year-old recruits comprised about 5–10 percent of the breeding population. There also appears to have been some net immigration of birds raised on Long Island, New York.

The rate of decline of this population has recently increased, from 3–4 percent per annum prior to 1969 to 8–10 percent per annum subsequently. No evidence exists for a significant decrease in the rate of recruitment to the population: the accelerated decline appears to be due to an increase in adult mortality, from about 9 percent to about 17 percent per annum. The earlier estimate by Austin and Austin (1956) of annual adult mortality in this population as 25–29 percent is apparently incorrect, as a result of biases introduced by band-loss and trapshyness.

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LITERATURE CITED

- Austin, O. L. 1942. The life span of the Common Tern (Sterna hirundo). Bird-Banding, 13: 159-176.
- ——. 1951. Group adherence in the Common Tern. Bird-Banding, 22: 1-10.
- Ms. Banding notebooks, 1929–57, and file of recoveries reported subsequently, at Massachusetts Audubon Society, Lincoln, Mass.
- Austin, O. L., and O. L. Austin, Jr. 1956. Some demographic aspects of the Cape Cod population of Common Terns (Sterna hirundo). Bird-Banding, 27: 55-66.
- Buckley, P. A., R. O. Paxton, and D. A. Cutler. 1975. Hudson-Delaware Region—Summer season, 1975. Amer. Birds, 29: 947-954.
- ——. 1976. Hudson-Delaware Region—Summer season, 1976. Amer. Birds, 30: 932–938.
- COOPER, D., H. HAYS, AND C. PESSINO. 1966. Breeding of the Common and Roseate Terns on Great Gull Island. *Proc. Linn. Soc. N.Y.*, 71: 105-118.
- Gochfeld, M., and D. B. Ford. 1973. Reproductive success of Common Terns on Jones Beach, Long Island, New York, in 1972: a hurricane year. *Proc. Linn. Soc. N.Y.*, 72: 63-76.
- LECROY, M., AND S. LECROY. 1974. Growth and fledging in the Common Tern (Sterna hirundo). Bird-Banding, 45: 326-340.
- NISBET, I. C. T. 1972. Disaster year for terns. Man and Nature, Dec. 1972: 16-21.
- —. 1973. Terns in Massachusetts: present numbers and historical changes. *Bird-Banding*, **44**: 27–55.
- ——. 1976. Returns from terns. Mass. Audubon Newsletter, 15(8): 3-5.
- NISBET, I. C. T., AND W. H. DRURY. 1972. Measuring breeding success in Common and Roseate Terns. *Bird-Banding*, 43: 97–106.

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