

BREEDING BEHAVIOR AND SUCCESS IN SALT MARSH COMMON TERN COLONIES

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INTRODUCTION

Common Terns (*Sterna hirundo*) traditionally nest on sand and shingle beaches, sand dunes, and on sand islands in freshwater and coastal marshes (Bent, 1921; Austin, 1929; Stone, 1937; Palmer, 1941; Cramp et al., 1974). Because people select these sites for swimming beaches, marinas, and private homes, Common Terns cannot always use them. Although Wilson (1854) noted that Common Terns nested on salt marsh islands in the mid-1800's, the extent of their occupation remained unknown. In 1976, we surveyed 46 miles of New Jersey coastline, finding 34 colonies on salt marsh islands, but none nested on salt marshes of the barrier islands. Certainly in New Jersey, and perhaps elsewhere on the Atlantic Coast (Drury, 1965; Nisbet, 1973) and in Europe (Greenhalgh, 1974), salt marshes contribute substantially to the production of Common Terns. In places such as New York with prospering dry land tern colonies, salt marsh colonies may serve as havens for mainland or barrier beach island colonies affected by human disturbance and mammalian predation (Austin, 1932a,b; Stone, 1937; Palmer, 1941).

We found few published accounts of salt marsh colonies of Common Terns, and no surveys of breeding biology on a series of colonies despite the occurrence of numerous studies on dry land colonies. If salt marsh colonies of Common Terns are to be successful, they must withstand high storm tides and avian predation. Common Tern colonies were studied on salt marshes to determine breeding chronology, habitat usage, and reproductive success. We were especially interested in synchrony among colonies and in the effect of high tides, heavy rains, and predators on reproductive success. Because extensive work on these colonies is essential for understanding their contribution to overall population levels, we wanted to determine the best time for sampling, as well as to try different sampling procedures.

STUDY ISLANDS AND METHODS

From 15 April to 15 August 1978, we studied 11 islands in Barnegat Bay, New Jersey: Little Beach, Petite, West Carvel, East Carvel, Log Creek, North Log Creek, West Vole, East Vole, Buster, Flat Creek and Cedar Creek (for details of islands, see Burger and Lesser, 1978). The islands ranged in size from 0.9 to 43 acres, contained 10% or less of windrow, and were primarily covered with *Spartina*. Most islands contained both *S. patens* and *S. alterniflora* although the percentage of each species varied. Higher areas of *S. patens* occurred on East Vole Is. where the local Mosquito Commission deposited spoil when they dug ditches. Still higher parts with shrubs, (*Iva* and *Baccharis*) occurred on West Vole, West Carvel, and Buster Is.

TABLE 1
Ratios of the number of flying birds to active nests in Common Terns.

Island	Maximum nests			Date					
	Date	Num-ber	Ratio	May 19	June 4	June 18	July 2	July 16	July 30
Log	18 June	43	1.2	—	1.4	1.2	3.0	2.2	—
E. Carvel	4 June	265	1.0	4.4	1.0	1.3	1.7	4.2	—
W. Vole	2 July	169	1.1	—	3.6	2.6	1.1	2.4	17.7
Flat Creek	18 June	14	2.1	—	—	2.1	2.4	2.0	—
Cedar	18 June	35	1.7	—	2.0	1.7	2.5	—	—
N. Log	4 June	27	1.3	—	1.3	2.1	3.5	1.5	—
Buster	4 June	38	2.6	—	2.6	2.8	—	—	—
Little Beach	18 June	42	1.1	20.0	1.6	1.1	1.3	—	—
E. Vole	4 June	252	1.3	14.3	1.5	1.5	1.3	2.1	—
Petite	2 July	94	1.0	—	1.6	1.0	1.1	1.1	17.7
W. Carvel	2 July	58	1.3	—	2.5	1.3	1.8	2.9	11.0

Each island was visited by boat every two weeks from 0600 to 1400. We counted the number of birds of all species that flushed as we arrived, and recorded the following information at every nest: contents, location with respect to vegetation, nearest neighbor distance, and species of the nearest neighbor. We defined an active nest as one with eggs and/or chicks. Because tern chicks over five to seven days old run and hide when disturbed, "nests with chicks" refers to nests with chicks under seven days. We also recorded the occurrence of nests clearly having older chicks being fed at the nest, the number of flying chicks, and chicks found away from nests.

All evidence of predation was noted including pecked eggs, remains of yolk, killed or eaten young or adults, and feathers. We also noted evidence of tide destruction such as washed out nests and eggs. Following a high tide and heavy rain storm (3–5 July) we surveyed and recorded the weights and wing lengths of randomly selected live and dead chicks.

RESULTS

Breeding Chronology

We found no evidence of nesting on any islands on 1–2 May. By 5 May, E. Carvel had three nests and by 19 May, laying had begun on E. Vole and Little Beach (Fig. 1). The initiation of laying on the 11 islands ranged from 5 May until 15 June with most colonies beginning in mid-May. The greatest number of nests occurred on the islands during the censuses from 4 June to 2 July (Table 1). The date of the peak of total nests present correlated negatively with maximum number of nests in the colony (Spearman's rank r : -0.48 , d.f. = 20, $P < .05$). That is, larger colonies had their peak number of nests earlier than did smaller colonies.

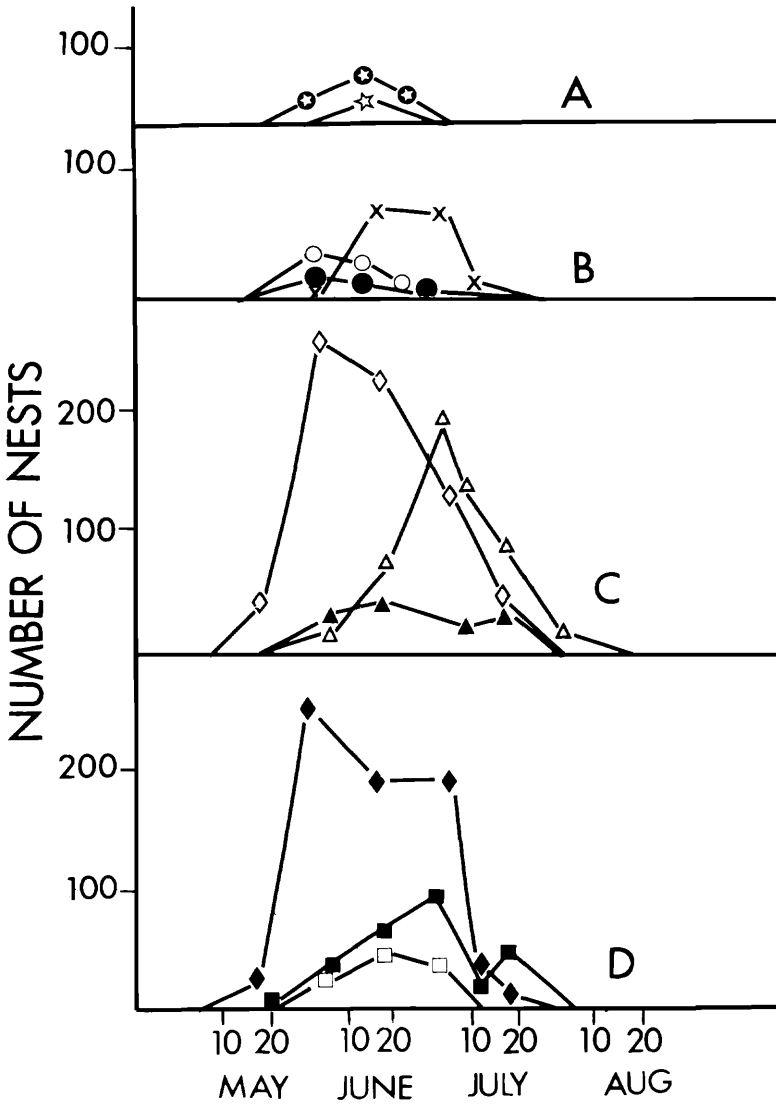


FIGURE 1. Number of active Common Tern nests per island during the nesting season. Shown from the top to the bottom are: Star in a circle = Cedar, Star = Flat Creek, X = W. Carvel, open circle = Buster, closed circle = N. Log; open diamond = E. Carvel, open triangle = W. Vole, closed triangle = Log, closed diamond = E. Vole, closed square = Petite, and open square = Little Beach.

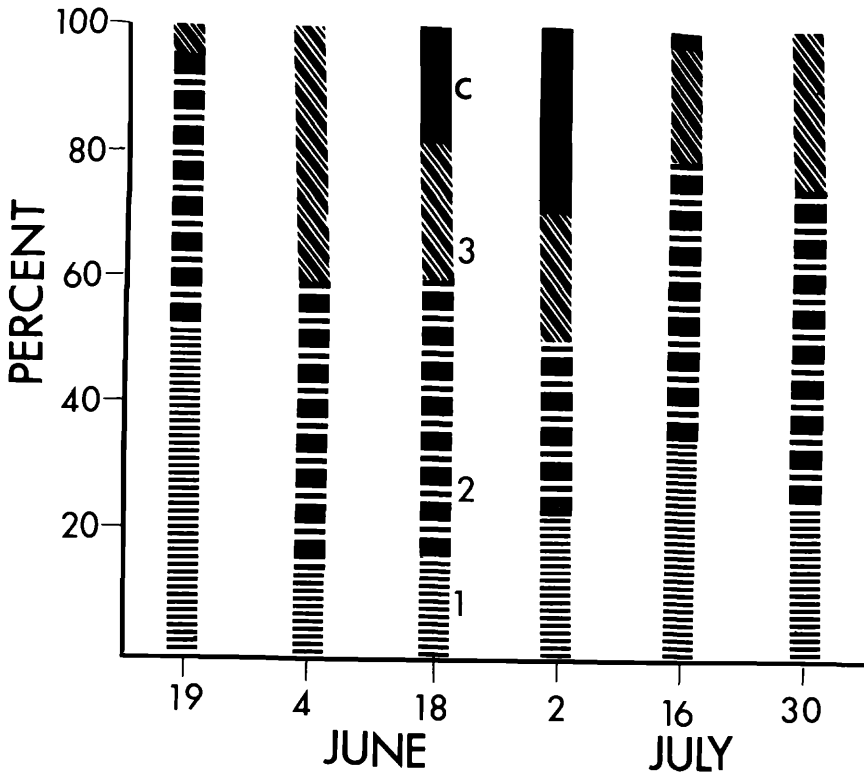


FIGURE 2. Cumulative percentage of nests with 1 (hatched), 2 (wide bars), 3 (diagonal bars) eggs or chicks (solid).

The number of active nests generally began to decrease in late June because of predation (see below) and hatching chicks reaching seven days of age. In early July a rain storm accompanied by high tides destroyed many eggs and young. Nest contents varied by date (Fig. 2). The number of 1-egg clutches was highest early and late in the season. The number of active nests with chicks one week old or younger was highest in late June and early July. Many of the clutches hatched following the 2 July sampling period, but these chicks hid in the grass and were not counted in the active nest category. After the storm in early July, the percentage of nests with eggs increased as birds relaid. The nests with chicks over seven days do not show up in Figure 2 because the chicks could not be assigned to specific nests. Mean clutch size reached a peak on 4 June, and decreased thereafter (Fig. 3). This figure includes data from all islands, so any loss of eggs by predation would decrease the overall mean clutch size. Eliminating data from islands with predation for 4 June increases the clutch size to 2.5.

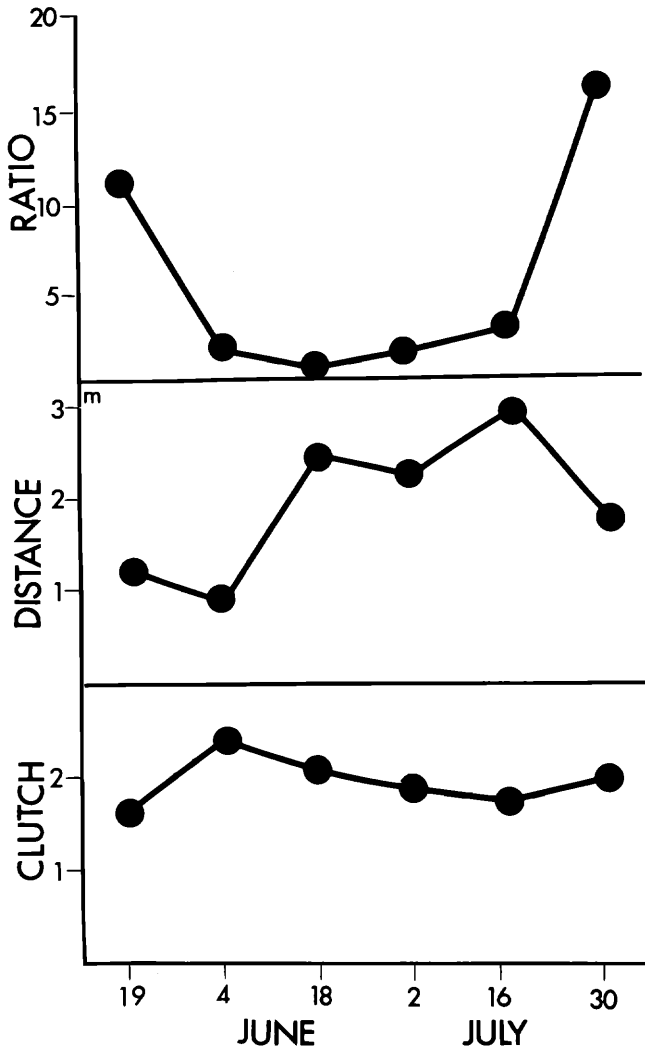


FIGURE 3. Mean clutch size, distance to nearest neighbor and ratio of flying adults to active nests.

We recorded the distance to the nearest neighbor to determine seasonal differences (Fig. 3). The mean distance to the nearest neighbor was lowest early in the season and increased until 16 July. Late nesting birds that relaid after losing their clutches in the storm, nested very close together. Most birds nested on windrow making colonies longitudinal because windrow is deposited along the shoreline.

The lowest nearest neighbor distance for any island occurred when the maximum number of nests occurred on that island ($r = -.56$, d.f. = 20, $P < 0.01$). That is, colony size was inversely related to nearest neighbor distance. For seven islands (W. Vole, Flat, Petite, N. Log, W. Carvel, Buster, and Little Beach), the lowest nearest neighbor distance occurred when the largest number of nests was present. On these islands, early nests were spaced out, and later nesting pairs filled in. For four islands (E. Vole, Cedar, E. Carvel, and Log), the lowest nearest neighbor distances occurred before the peak of nesting. On these islands early nesters nested close together in one (Cedar Island) or several epicenters (E. Vole, E. Carvel, Log), and later pairs nested farther apart adjacent to the epicenters. Thus, on all islands the lowest neighbor distances occurred before or at the peak of nesting.

During each sample period we recorded the number of terns flushed as we approached. We then divided the number of flying adults by the number of active nests and computed a mean of the survey data from all islands (Fig. 3). In early May the ratio was 10.9, and in late July it was 15.1; but from 4 June to 16 July it averaged 1.2 to 2.4. The ratio decreased in June and early July when most adults were incubating. The storm in early July wiped out most nests and most adults remained in the colony area for several weeks without having nests. For large scale sampling of many colonies, sampling can occur over a two-week period in early June with a ratio of 1.2.

Table 1 gives the ratios for individual islands as a function of date. With respect to individual islands, the ratios decreased until the peak of active nesting, and generally increased thereafter. The highest ratios for peak nesting periods occurred on islands (Flat Creek and Buster) having high predation rates over a short period of time resulting in rapid abandonment. Perhaps these colonies never reached their possible peak number of nests. For some islands (N. Log, Log), the ratio decreased toward the end of the season reflecting the abandonment of the colony by unsuccessful birds.

Habitat Selection

Common Terns prefer to nest on islands containing wrack (Burger and Lesser, 1978). A wrack or windrow is dead vegetation, either *Zostera* or *Spartina*, strewn on the marsh by high tides. Exceptionally high tides in April removed much of the wrack, forcing these birds to move to other islands. The islands' terns moved to contained low places of *Spartina alterniflora*, with higher spots of *S. patens*. Wrack, which can occur on either vegetation, is away from the edges of islands on the higher elevation spots.

For all islands we summed the number of nests on wrack, *S. patens* and *S. alterniflora*, and computed the mean percentage in each habitat as a function of date. The percentage of nests on wrack decreased to 60% by early June, increased to 65% by early July, and increased to

TABLE 2
Predation rates prior to and following the storm.

Island	% predation before storm	% chicks killed	% nests destroyed	Mean number ¹ fledged per nest
Buster	100	0	0	.00
Flat Creek	80	80	100	.07
N. Log	76	(none hatched)	71	.00
W. Vole	46	38	24	.02
Petite ²	0	81	93	.00
Cedar Creek	38	60	100	.14
Little Beach	4	100	100	.00
W. Carvel	4	83	7	.02
Log Creek ²	0	71	31	.09
E. Vole	0	48	8	.92
E. Carvel	0	35	41	.96

¹ Calculated on the basis of the maximum number of nests per colony.

² Suffered 100% predation of all nests remaining after the storm.

100% by mid-July. Even on 4 June when the least number of nests were on wrack, terns significantly selected wrack compared to the habitat available ($\chi^2 = 732$, d.f. = 3, $P < .001$). In the middle of the nesting season, terns nested in *S. patens* 20% of the time, in *S. alterniflora* 8% of the time, and in other vegetation (primarily *Phragmites*) 18% of the time.

In summary, in 1978 terns nested on previously used islands and preferred to nest on wrack. Most terns nested on wrack early and late in the season. During the peak of nesting, the amount of wrack was insufficient for the number of terns and more nested in *Spartina*. The habitat used on individual islands varied depending on the availability of wrack or of other high spots (such as *S. patens*). Without these high places, some terns nested in lower *S. alterniflora*.

Reproductive Success

Reproductive success in any Common Tern colony, either salt marsh or dry land, depends upon such factors as food availability, parental behavior, storms, high tides, and predation. The 11 tern colonies we examined had different reproductive successes. Several islands suffered high predation rates early in the season. Buster Is. had an active colony in 1976 (287 nests), failed in 1977 because of high storm tides, and was completely wiped out in 1978 by predators. The 38 nests in wrack were intact on 4 June, but by 18 June, 45% of the nests had been destroyed, the eggs eaten, and one adult partially eaten. We saw a Great Black-backed Gull (*Larus marinus*) with an egg in its bill, and Herring Gulls (*L. argentatus*) regularly entered the colony. A new colony then formed in wrack and *Spartina* some distance from the original colony. The nests

TABLE 3
Effects of heavy rain and storm tides on breeding success as a function of habitat.

	A. Percent washed out nests		
	Wrack	<i>S. patens</i>	<i>S. alterniflora</i>
E. Carvel	21		83
E. Vole	56	62	100
W. Vole	15		80
W. Carvel	14		
Petite	18	62	
Log Creek	27		
	B. Percent chick deaths		
	Wrack	<i>S. patens</i>	<i>S. alterniflora</i>
E. Vole	100	42	32
Petite	92	50	
W. Carvel	77		88
E. Carvel	39		34
W. Vole	38		

in the new colony were significantly ($t = 5.94$, d.f. = 23, $P < .01$) farther apart ($\bar{x} = 165 \pm 63$ cm) but by 4 July all nests were destroyed.

Cedar Creek also suffered predation. We found missing eggs as well as a beheaded adult next to a Barn Owl (*Tyto alba*) feather. This colony, destroyed partially (38%) by predation, was inundated by the high tides of early July. Only five young fledged from 35 nests.

N. Log suffered 76% predation by 3 July when the tides wiped out the rest of the nests. Flat Creek suffered 80% predation between 18 June and 2 July. W. Vole suffered 100% predation of 45 nests near the Herring Gull colony. We saw Herring and Great Black-backed gulls eating tern eggs and suspect herons and owls as well.

Thus, predation resulted in the total destruction of one colony, over 75% predation in two colonies, and 100% predation in nests near a Herring Gull colony in another.

High tides accompanied heavy rains from 3–5 July when more than 12 cm of rain fell during a five-hour period. Table 2 shows the destruction of chicks and nests. We computed the percentages on the basis of the number of nests present on 2 July. To compute chick figures we searched each colony thoroughly. For all islands, 46% of the chicks died during the storm and 30% of the nests were washed out. Some colonies completely succumbed to the storm (Little Beach, Flat Creek), whereas others fared better.

Habitat affected survival. For all islands combined (Fig. 4), fewer nests washed out in wrack compared to other habitats ($\chi^2 = 62.2$, d.f. = 2, $P < .001$). However, more chick deaths occurred on wrack compared to the other habitats ($\chi^2 = 10.2$, d.f. = 2, $P < .05$).

The percent of washed out nests varied by island as well as habitat (Table 3). Washouts on wrack on E. Vole were high because the wrack

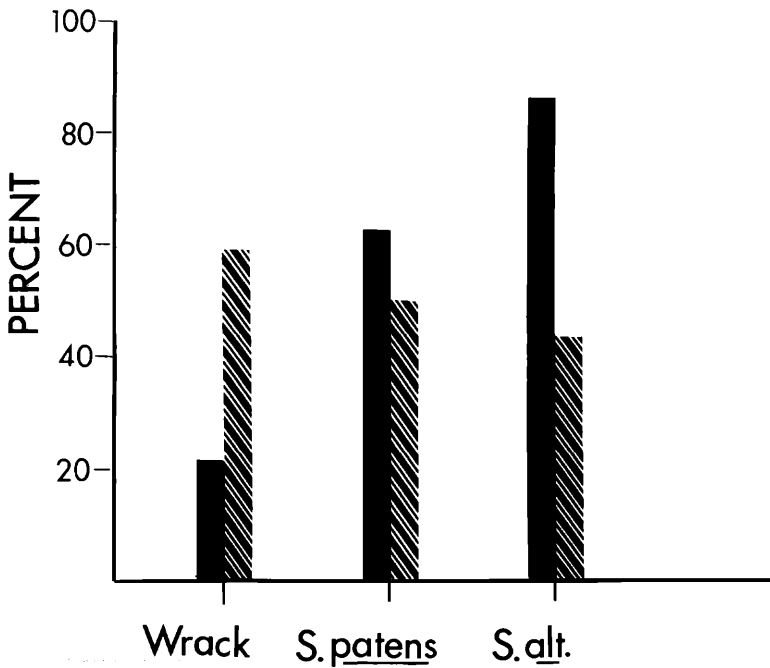


FIGURE 4. Percent of nests washed out (solid bar) and chicks killed (diagonal bar) following the storm tides.

was low. Washouts on Log Creek and E. Carvel were intermediate because the wrack was higher on the marsh and away from the island edge. Few washouts occurred on the very high wrack of W. Carvel and W. Vole.

Chick deaths also varied by island and habitat (Table 3). The highest death rates occurred on E. Vole and W. Carvel. Chick survival also depended upon their size. The mean weight of live chicks ($\bar{x} = 119.3 \pm 7.9$ g) was significantly greater ($t = 9.16$, d.f. = 28, $P < .001$) than that for chicks that died ($\bar{x} = 65.1 \pm 24$ g). Similarly, the wing length of live chicks ($\bar{x} = 155.9 \pm 18$ cm) was significantly greater ($t = 9.61$, d.f. = 28, $P < .001$) than for chicks that died ($\bar{x} = 76.1 \pm 32$ cm). Although slight overlap occurred in the weights and wing lengths of chicks that died and lived, when the two factors are considered together, no overlap occurred (see Fig. 5).

Because of predation and high tides, the production per nest ranged from 0 to 0.96 (Table 2). However, these figures are minima because we divided the number of fledged flying young by the maximum number of nests on that island, and some young may have left the island undetected.

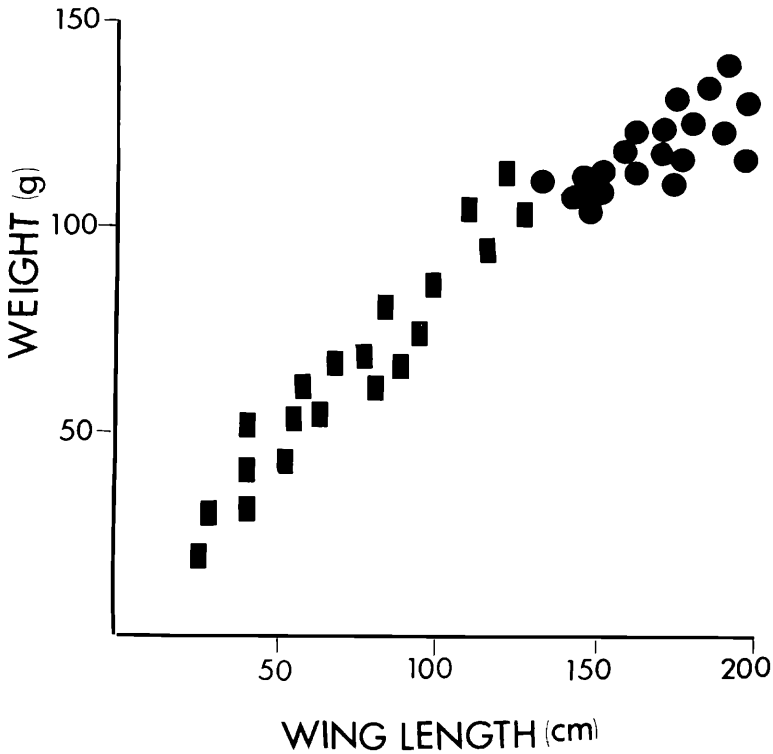


FIGURE 5. Common Tern chicks that survived (circles) and died (squares) as a function of wing length and weight (after 3-5 July storm).

DISCUSSION

Breeding Chronology

Nest initiation in the 11 colonies began over a one-month period from 5 May until 4 June, with peak number of nests extending from 4 June to 2 July. The number of active nests tapered off to zero by the end of July, and no later nesting occurred. Despite extensive research on the breeding biology of Common Terns nesting on dry land (Austin, 1932, 1933), no published breeding chronologies exist for several colonies in one year. Usually authors report dates in which eggs or young occurred in particular colonies (Bent, 1921; Stone, 1937). Most authors report that fresh eggs can be found in colonies from late May until late July, with a peak early in the season (Austin, 1933; Nisbet, 1973). Nisbet (1973) summarized this information from dry land colonies, and several differences exist with our marsh colonies: (1) the peak in the number of nests varied markedly from early June to early July and did not occur in May, (2) only one of 11 colonies had a secondary peak in the number

of nests following the major peak, (3) major shifts from one colony to another did not seem to occur following decreases due to predation, and (4) no major relaying attempts occurred in late July after the devastating effects of high tides.

These differences relate directly to tidal conditions in the salt marshes. The range of dates for colony formation were affected by tides. For some islands, high water during May prevented early colonization. Although all occupied islands in 1978 were used in 1977 and 1976, the number of pairs varied considerably. For example, E. Vole had only one nest in 1976 and 252 in 1978, and N. Vole had 55 in 1976 and 169 in 1978. E. Vole was slightly higher than many of the other islands. Its elevation could be judged by the high percentage of *S. patens* compared to several of the other islands. *S. patens* grows in higher places less exposed to tides than does *S. alterniflora* (Bourn and Cottam, 1950). The relatively high reproductive success on E. Vole compared to the other islands attests to the importance of marsh elevation.

The lack of relaying in nests destroyed by the early July storm in the salt marsh colonies is different from dry land colonies (Nisbet, 1973; M. Gochfeld, pers. comm.) where large numbers of terns may relay and successfully raise young in August. Hurricanes may ravage these salt marshes in August, washing over entire islands. Consistently, late nesters may never successfully raise young.

Variations in the peak number of nests occur because some islands are inundated by high tides early (W. Vole, E. Carvel) whereas others are not. The Clam Is. colony, active in 1976 and 1977, never did form in 1978 because the site was under water during May and early June. Terns flew over the site frequently in late May and early June but left in mid-June without nesting. The presence of many potential colony sites with active nests provides a number of alternatives in high tide years. Birds displaced from inundated islands can quickly move to a colony site suitable in terms of having existed for several years. Birds moved to sites that still contained nests. Since such islands had not become inundated by high tides, the new site was higher and drier. Thus, an abundance of colonies smaller than usual for dry land habitats is adaptive in presenting alternatives during flood years. One large colony could be wiped out easier by high tide than several smaller colonies on several different islands. Even in a disastrous tide year such as 1978, the range of islands selected allowed production in seven of the 11 colonies.

Larger colonies had significantly earlier nesting peaks than smaller colonies which agrees with the controversial Darling effect (1938). The Darling effect has not been adequately tested despite frequent references to it in the literature (see Coulson and White, 1956 for a review). Previous studies have tended to compare colonies between years rather than within years but because weather and habitat factors vary from year to year, data must be collected in one year to insure meaningful comparisons.

These data from salt marsh colonies suggest many difficulties in determining the right time to survey for accurate counts. Whereas during the peak of nesting the ratio of the number of flying adults to the number of nests was low (1.0 to 2.6), it was not as low or consistent as the 1.1 reported by Nisbet (1973). Our higher ratios occurred in colonies suffering high predation (Buster) or tidal inundation (Flat Creek) before they reached their potential peak. Applying a 1.1 ratio overestimates the number of nests in colonies with high predation because some birds would desert even before laying eggs. Tides destroy some nests, and are also a factor in raising the ratio. It may not be possible to be as accurate with only one sampling period in salt marsh colonies compared to dry land colonies.

Buckley et al. (1977) compared one helicopter survey with ground counts over the entire season for two tern colonies during four years. These colonies had 1,800 to 3,300 nests during the sample years. High tides never forced the terns to abandon either site or to suffer total destruction. They recommended multiplying the number of flying terns by 0.92 to obtain an estimate of the number of nests. Theirs is the best test of sampling procedures for a larid and should serve as a model for future study. Had we selected the two largest and most stable colonies (E. Carvel, E. Vole) for study, we would have obtained more consistent data, because the presence of so many small colonies increased the variability in breeding chronology.

The number of adults hovering over colonies may indicate the number of pairs attempting to breed. High tides and predators may force pairs to forego breeding at that location or during that year. Thus our ratios, when they differ from 1.1 may reflect the number of birds unable to start breeding. The difference, those that failed even to attempt nesting, would be more difficult to determine in dry land colonies. Nisbet (1973) reported large numbers of nonbreeding adults in resting flocks at the edge of colonies, but we did not observe such resting flocks in salt marsh colonies. Of course, no open sandy places exist, and nonbreeding birds may remain on ocean beaches rather than back in the salt marshes.

Habitat Preferences

The terns on the islands surveyed generally nested on wrack earlier, nested on wrack and *Spartina* during the peak of nesting, and on wrack later in the season. We believe this reflects the amount of wrack rather than preferences. Because of high tides in May, terns nested first on high wrack and moved into *Spartina* only when wrack was unavailable and tide waters had receded. Some early nesting terns nested in *Spartina* areas on West Carvel and Petite. But these areas had only scattered *Spartina* stems since the terns nested where the wrack had been removed by high tides. These pairs attempted to nest where they had in previous years, and the wrack was simply no longer there. Colony and nest site tenacity have been shown for a number of larids (Austin and Kuroda,

1953; Tinbergen, 1956; Vermeer, 1963; Brown, 1967; Bongiorno, 1970; McNicholl, 1975).

Breeding Success

In the present study, breeding success was determined by dividing the number of young fledged by the maximum number of nests in the colony. This is an underestimate because some young may have escaped our counting by hiding in the vegetation or leaving the colony without our knowledge, but nests were easily counted. Success figures are difficult to compare because authors often do not state how they defined success, and these figures are never for salt marsh habitats (Langham, 1972; Lemmetyinen, 1973). Success on the surveyed islands ranged from 0 to 0.96 young fledged per nest. The two largest colonies had the highest success. The causes of low reproductive success, predation, and tidal effects acted separately and together. Predation alone wiped out only one colony. Otherwise predation rates prior to the high tides eliminated 0 to 80% of the nests. Four colonies (Table 2) seemed to suffer no discernible predation prior to the storm. The storm and tides then wiped out, or finished wiping out, five colonies (N. Log, W. Vole, Little Beach, W. Carvel, Flat Creek). The birds in these colonies never relaid. We surveyed by helicopter all salt marsh islands along 46 mi of coastline, and found no new colonies during the month after the storm. On two islands (Log, Petite), an interesting pattern developed whereby nests and eggs did not suffer predation before the storm; they were not wiped out by the storm but they were subsequently wiped out by the terns themselves. Eggs were not pecked by American Oystercatchers (*Haematopus palliatus*), gulls or herons. The peck holes were tern-like, destruction occurred all at once, and we saw terns pecking some eggs. It seemed as if the colony "fell apart" following the devastating destruction by tides. The remaining pairs no longer behaved normally with respect to mobbing gulls or humans. Thus, colonies partially destroyed by tides seem more vulnerable to predators.

Predation rates were higher in smaller colonies. Salt marsh colonies seldom have ground predators because winter storm tides make survival difficult for mammalian predators. Thus, avian predators such as gulls and owls account for predation in these colonies. Nests densely packed on wrack are highly visible to aerial predators. Terns responded to predation pressure by moving to *Spartina* and nesting significantly farther apart on Buster Island. This strategy was ineffective because the new colony also suffered predation, but the numbers had already dwindled, and perhaps too few terns remained for adequate mobbing behavior. The importance of sufficient numbers of birds for successful mobbing has been discussed for larids (Kruuk, 1964; Patterson, 1965; Tinbergen et al., 1967; Lemmetyinen, 1971, 1972, 1973; Montevecchi, 1977). The potential avian predators (crows, gulls, herons, and owls) are well known predators on larids (Buckley and Buckley, 1972; Burger, 1974; Nisbet, 1975; Hunter and Morris, 1976; Montevecchi, 1977; Burger and Lesser,

1978). In this study, gulls provided the greatest threat to tern colonies, particularly when gulls and terns nested next to one another. Adjacent nesting resulted in nearly 100% predation, whereas increasing the distance between these colonies decreased predation. The recent expansion of Herring Gulls in the eastern United States (Hailman, 1963; Drury, 1965; Kadlec and Drury, 1968) and their invasion into salt marshes (Burger, 1977) poses a significant threat to tern colonies.

The most important causes of low reproductive success in most colonies were the high tides and heavy rains of early July. All active colonies lost some eggs and chicks during the storm. Washouts seem directly related to the severity of the tides and nest height. Fewer washouts occurred on wrack than in *Spartina*. *Spartina patens* grows at the same relative elevation on different islands, but some variation exists. For example, on an island in the middle of the bay, *S. patens* does not grow at as low elevations as elsewhere because frequent storm waves build up higher in the open bay, whereas this would not occur in the protected islands directly behind barrier beaches. Tides reach farther on islands exposed to the prevailing direction of the wind. Thus, the occurrence of many colonies scattered around Barnegat Bay insures that some remain safe from the vagaries of wind direction.

In this particular storm, both high tides and heavy rain caused destruction. On wrack only 21% of the nests with eggs washed away, so it seems reasonable to assume that only 21% of the nests with chicks would have washed away. Yet 58% of the chicks on wrack died. The high tides preceded the heavy rains by several hours. We believe that exposure to 12 cm of rain in five hours accounted for the differences between chick deaths and egg loss. Fewer chick deaths occurred in *Spartina* because the grass provided protection from rain. With higher tides, the mobile chicks in the grass could seek higher wrack. When the tides receded, chicks returned to their nests in the grass and were protected against the heavy rains. Austin (1933) stressed the importance of cover to Common Terns during rain because storms and wind often result in higher tides.

The largest, heaviest chicks survived the storm. Some chicks weighing 95 to 120 g died whereas other lived. Perhaps chicks in this range are too large to be brooded, and too small to withstand extensive exposure to cold rain. Some parents may brood whereas other do not. Perhaps parents with two and three chicks could not brood them all. Since we could not determine brood size, we could not fully evaluate this factor.

SUMMARY

Eleven salt marsh colonies of Common Terns initiated egg-laying from early May until early June 1978, with peaks in the maximum number of nests per colony from early June until early July. Larger colonies had earlier peaks than smaller colonies. The ratio of the number of flying adults to the number of nests in any colony varied seasonally, but was generally highest early and late in the season. The lowest average

ratios for all colonies were obtained on 4 June. Tidal and predation effects increase the ratio making it difficult to predict from these ratios exactly how many nests were present. Predation alone wiped out only one colony. Otherwise, predators destroyed 0 to 80% of the nests in 10 colonies. Four colonies suffered no predation prior to the storm, which eliminated five colonies completely or nearly so. Following the storm, Common Terns eliminated two colonies by puncturing eggs. Only two colonies had a fledging rate approaching one chick per nest. Small to medium sized Common Tern colonies in salt marshes seem to provide a variety of conditions so that some young fledge from some colonies every year.

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