

## VIABILITY OF SALT MARSHES AS NESTING HABITAT FOR COMMON TERNS IN NEW YORK<sup>1</sup>

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*Abstract.* We examined Common Terns (*Sterna hirundo*) nesting between Jones and Fire Island inlets on the barrier beach and salt marshes of the south shore of Long Island, New York during 1986 and 1987. Controversy exists in the literature over whether beaches and salt-marsh islands are traditional nesting areas offering alternative viable breeding sites for Common Terns, or whether salt marshes are suboptimal habitat into which Common Terns are largely 'forced' after loss of beach habitat. Past studies usually compared geographically distant sites, thus introducing uncertainty about the role of local climatic and food conditions in affecting reproductive variables. We tested the null hypothesis that reproductive success does not differ between habitats for colonies bordering the same estuarine system. Interyear and intercolony differences were strong, and interhabitat differences were inconsistent. Despite generally lower hatching success and generally greater nest destruction in salt marshes, tern pairs in both habitats fledged similar numbers of chicks of similar sizes and weights. Movements of birds banded on beaches and in marshes indicated that birds tended to breed in the same habitat in which they hatched, and that breeding adults were likely to nest subsequently in the same habitat.

*Key words:* Common Tern; *Sterna hirundo*; salt marsh; breeding success; habitat.

### INTRODUCTION

In the mid-Atlantic coastal U.S., barrier beaches have been thought to be the most important sites for Common Tern colonies, and most studies have focused on this habitat (Buckley and Buckley 1982a). Since the mid-1970s increasing attention has been drawn by colonies in salt marshes (e.g., Nisbet 1973; Burger and Lesser 1978, 1979; Buckley and Buckley 1980, 1982a). Prior to this, although scattered references to marsh-nesting terns could be found (e.g., Wilson 1854, Drury 1965), the degree to which Common Terns (*Sterna hirundo*) used salt marshes was not known. Buckley and Buckley (1980) were "quite unprepared for the large numbers we found nesting in Long Island marshes in 1974." Either a substantial portion of marsh colonies had been overlooked, or the terns had recently begun to increase their use of this habitat. Each year roughly 20-25% of Long Island's Common Terns nest on salt-marsh islands (Buckley and Buckley 1982b). In New Jersey, where beaches are heavily developed, almost all Common Terns nest on salt-marsh islands (Buckley 1979, Burger and Lesser 1979, Erwin et al. 1981).

Several researchers have viewed Common

Terns as being recent invaders of salt marshes, forced there by coastal development, and have discussed salt marshes as suboptimal breeding sites (Burger and Shisler 1979, Buckley 1979, Erwin et al. 1981). Erwin (1980) noted that it was unknown whether Common Terns were able to reproduce as successfully in marsh habitats as on barrier beaches. Although Erwin and Smith (1985) found that interyear and intercolony effects on reproduction were greater than interhabitat effects, they believed that Common Terns preferred barrier beaches in southern New Jersey and Virginia, and that terns nesting in marshes had been displaced from beaches by human activity.

Comparisons of colonies physically or temporally distant from one another are potentially confounded by weather differences and fluctuations in food availability, which can be significant in affecting reproduction (Safina et al. 1988). We undertook this study to compare the reproductive success of terns nesting in barrier-beach and salt-marsh colonies within the same estuarine system during the same time period. Had we wanted to strictly study the effects of habitat on nesting terns, we would have chosen colonies which were as similar to each other as possible. But because we wanted to study the viability of salt-marsh colonies relative to beach colonies, we sought to include all the colonies in our study

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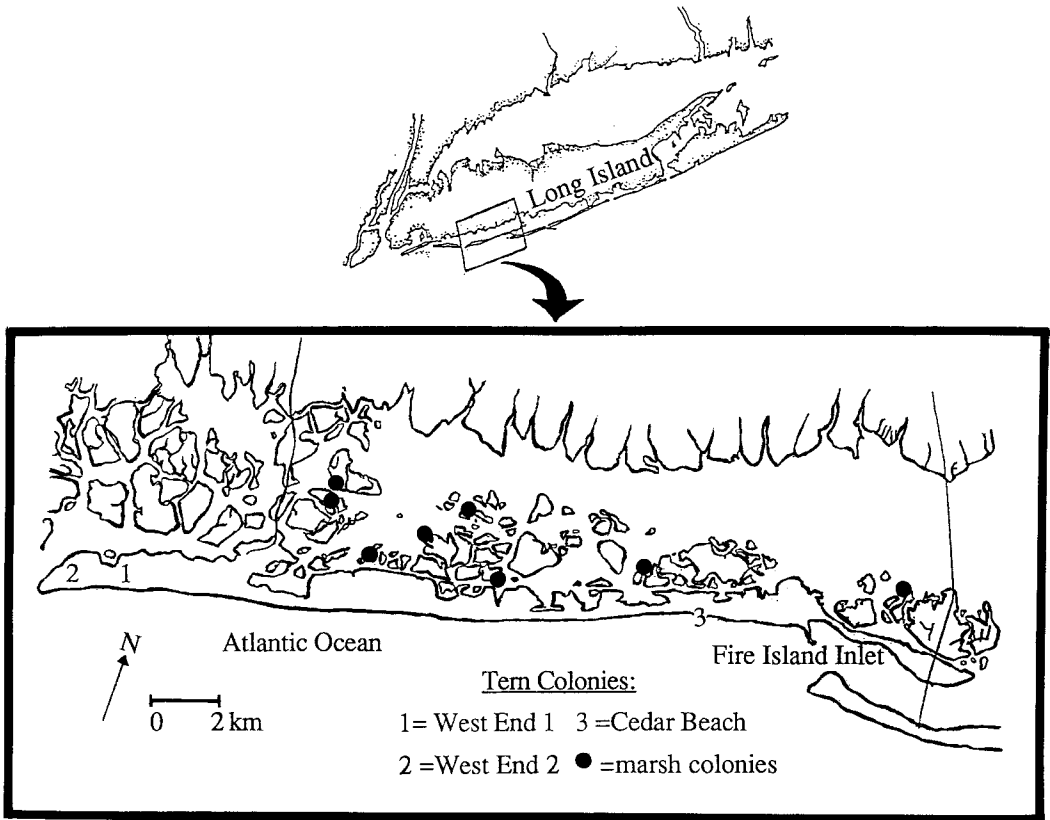


FIGURE 1. The study area on the south shore of Long Island, New York.

area. These colonies were diverse in size and history, and well represented the diversity which generally exists among colonies in these habitats. We tested the null hypothesis that reproductive success did not differ significantly between habitats.

#### STUDY AREA AND METHODS

We monitored breeding Common Terns in barrier-beach and salt-marsh colonies between Jones Inlet and Fire Island Inlet on the south shore of Long Island, New York (40°N, 73°W; Fig. 1) from May through July in 1986 and 1987.

All three colonies on the barrier beach were monitored (Fig. 1, Table 1). West End 2, located in and around the western turnaround loop of Ocean Parkway, has declined from approximately 2,500 pairs in the late 1970s due to disturbance and predation, especially by dogs from the nearby Coast Guard station. West End 1 was first colonized by Common Terns in 1986, partly by birds which formerly bred at West End 2 (ca.

1 km west). Although the colony is close to a bathing beach, fencing and posting by the National Audubon Society and the State Parks Commission have been effective in reducing human disturbance. Cedar Beach is on a barrier-beach site composed of dredged fill. The number of birds here has doubled from approximately 2,500 pairs in the late 1970s, perhaps due in part to reduced human disturbance following posting and fencing by the Town of Babylon and National Audubon Society. Eight marsh colonies were monitored (Fig. 1, Table 1). Mosquitoes, biting flies, and mud make salt marshes subject to little human intrusion.

Beginning in early May, barrier-beach colony sites and all marsh islands between the Robert Moses Causeway and the Wantagh Parkway (Jones Beach Causeway) were checked for breeding terns. We attempted to monitor breeding on all marsh islands with nesting terns. This was accomplished except in one small colony (ca. 15 pairs) where surrounding shallows and mud pre-

cluded consistent boat access, and where nests were very widely scattered. Despite this, we collected data from over 95% of the salt-marsh nests in the study area. Some marsh colonies were studied in only 1 year because birds largely abandoned some and colonized others. Monitored colonies were visited every other day or as weather permitted.

Due to the size of the Cedar and West End 1 colonies we monitored nests in randomly selected sample plots. We estimated the total number of pairs of Common Terns nesting in the large beach colonies by: (1) counting all nests in each colony just prior to the beginning of hatching, and (2) adding to this count the percent increase in the number of nests in the regularly monitored sample plots between the day of the colony-wide count and the end of the major wave of egg laying. In salt marshes, we attempted to monitor all nests in the colonies where we worked.

To obtain data on breeding phenology, clutch size, and hatching success, one or two persons walked through the monitored areas marking new nests and recording number of eggs and chicks in each nest. Vegetation on which nests were placed was noted. Egg length and width was measured for 1,463 eggs in completed clutches in eight colonies. Egg volume was calculated using  $(\text{length})(\text{width}^2)/1,000$  (Miller 1979). To obtain data on intercolony movement of previously banded birds, adults were trapped during late incubation in all monitored colonies in both years.

To monitor chick growth and fledging success, we surrounded nests (on beaches  $n = 133$ , in marshes  $n = 65$ ) with 2.5-cm hexagonal mesh-wire fences approximately 0.3 m high prior to hatching (Nisbet and Drury 1972). Each fence had a 10-cm band of fine mesh fiberglass screen along the bottom to prevent newly hatched chicks from leaving fenced areas. Each fence was large enough to facilitate landing and takeoff of adults and incorporated vegetation for chicks' shade and cover. Fence diameters ranged from approximately 3–6 m.

Chicks inside fences were banded within 1 day of hatching and were checked every other day after hatching. We recorded wing length (to the nearest 2 mm) and weight to the nearest gram (using a Pesola spring scale) until death or fledging. Chicks were considered fledged if they had survived to at least 20 days of age before disappearing from the fences (soon after that age they acquire the ability to fly out). An inconsis-

TABLE 1. Common Tern colonies in this study.

	Estimated no. pairs	
	1986	1987
<b>Barrier beaches</b>		
West End 2	11	28
West End 1	268	1,923
Cedar Beach	5,023	6,509
Subtotal	5,302	8,460
<b>Salt marshes</b>		
Seaganus Thatch (4 subcolonies)*	780	358
West Gilgo	22	19
Island NW of Tobay Tower (Fishing Hat Island)	38	30
Tilted Log	0	96
North Line	38	15
Middle Line	117	104
Islands E of West Island (2 subcolonies)	300	180
Island W of Fox Creek	0	141
Subtotal	1,295	943
Grand total	6,597	9,403

\* Groups of nesting birds on closely adjacent islands were considered subcolonies of a main colony if they regularly interacted socially in mobbing us.

tency in the precision of a scale used to weigh chicks in 1986 was not discovered until after the breeding season, so all growth data from 1986 were deleted from our analysis.

Subsequent to most breeding activities, nest height (defined as the vertical distance from nest substrate to nest rim) was measured in all monitored colonies for 100 nests in each of the two habitats. In marshes, the number and dimensions of dead vegetation mats were measured on 15 islands with tern colonies and on 15 islands without terns. Nearest-neighbor distances were measured for 100 beach nests and 138 marsh nests. To examine characteristics of marsh islands used by terns, island area, mean depth around islands, distance to nearest island, distance across open bay to land, percent of island perimeter exposed to open bay, and distance to well-trafficked, deeper channels were determined from nautical maps for all islands between the Robert Moses Causeway and Wantagh Bridges.

Data were analyzed using SAS, SPSS, and Statgraphics statistical software. All data were checked for normality of distribution. Growth data were normalized by log-transformation prior to analysis. *F*-values refer to SAS General Linear Models procedure for unbalanced ANOVA unless otherwise noted. Tukey's studentized range

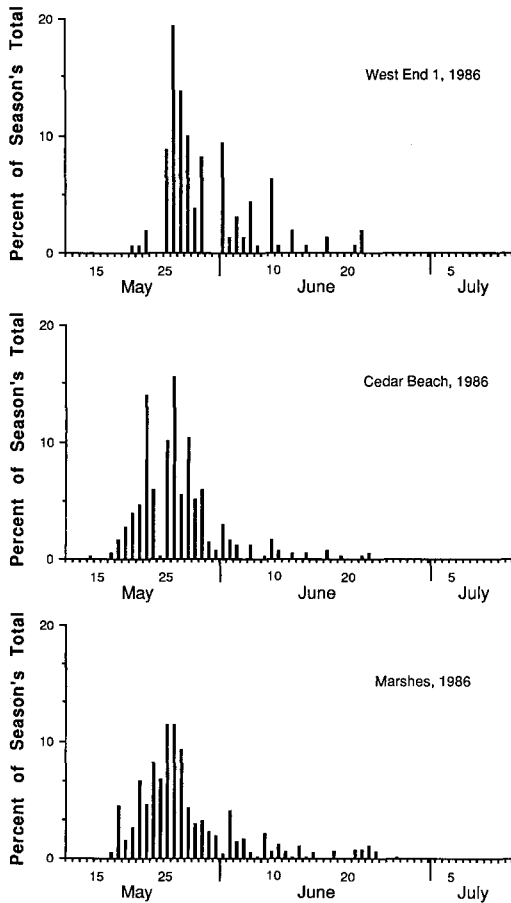


FIGURE 2. Phenology of clutch initiation in 1986. Percents refer to seasonal total number of clutches within each colony.

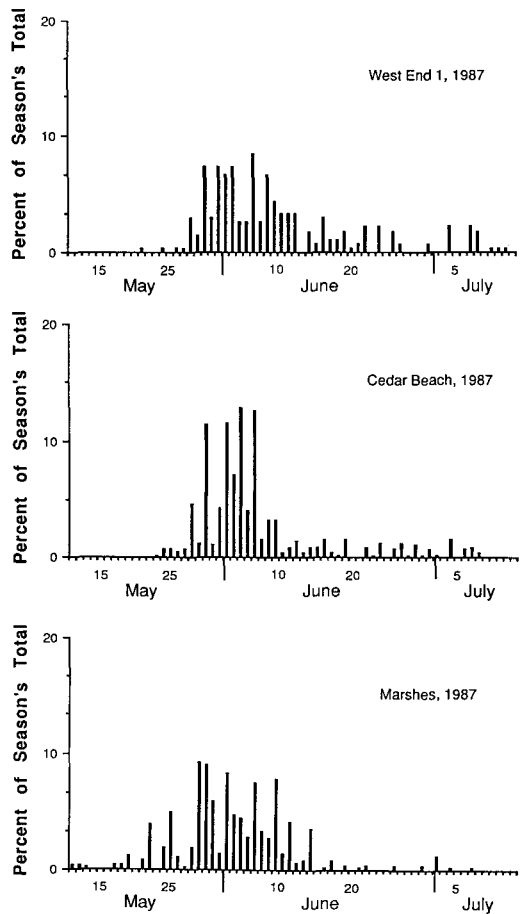


FIGURE 3. Phenology of clutch initiation in 1987. Percents refer to seasonal total number of clutches within each colony.

test was used for multiple comparisons. An alpha level of 0.05 was used to judge significance of tests.

**RESULTS**

In the colonies studied, the numbers of breeding Common Terns increased nearly 40% between 1986 and 1987. Populations in beach colonies increased by almost 60%, while marsh colony populations declined by approximately 40% (Table 1). For most variables measured, we found a high degree of variability between beach and marsh habitats, between years, and among all colonies.

**EGG LAYING THROUGH HATCHING**

*Clutch initiation.* Egg laying occurred later on beaches than in marshes, but this was largely due

to a difference in 1987; laying dates were not significantly different in 1986 (Figs. 2 and 3, Table 2). Among all colonies, habitat (beach vs. marsh) did not consistently affect laying dates, and there was much variability among colonies. For pooled data from both years, Tukey's multiple comparison tests following ANOVA indicated that laying dates differed significantly among several colonies: (1) one marsh colony was later than Cedar Beach, (2) four marsh colonies differed significantly from other marsh colonies, (3) four marsh colonies were earlier than either Cedar Beach or West End 1 beach, and (4) West End 1 was later than Cedar.

*Internest distances.* Mean nearest-nest distance was greater in marshes than on beaches ( $3.19 \pm 3.5$  m vs.  $2.23 \pm 1.5$  m, respectively;  $F = 6.7$ ,  $df = 237$ ,  $P < 0.01$ ). Among all colonies,

TABLE 2. Habitat comparisons for Common Tern reproductive parameters from egg laying through hatching. Means are per nest. SAS General Linear Models Procedure was used to compare means.

	Marsh		Beach		Rank order	F	P <
	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n			
<b>Clutch initiation</b>							
Both years	29 May $\pm$ 8	1,139	2 June $\pm$ 10	1,449	Beach > marsh	39.2	0.0001
1986	27 May $\pm$ 8	653	27 May $\pm$ 6	602	=		ns
1987	2 June $\pm$ 8	486	6 June $\pm$ 10	847	Beach > marsh	67.0	0.0001
<b>Clutch size</b>							
Both years	2.26 $\pm$ 0.6	1,907	2.10 $\pm$ 0.6	2,078	Marsh > beach	64.7	0.0001
1986	2.29 $\pm$ 0.7	1,127	2.13 $\pm$ 0.6	1,048	Marsh > beach	40.4	0.0001
1987	2.21 $\pm$ 0.6	780	2.07 $\pm$ 0.6	1,030	Marsh > beach	23.1	0.0001
<b>Eggs hatched</b>							
Both years	1.71 $\pm$ 1.0	1,647	1.94 $\pm$ 0.8	1,646	Beach > marsh	53.0	0.0001
1986	1.70 $\pm$ 1.0	904	2.07 $\pm$ 0.8	775	Beach > marsh	68.1	0.0001
1987	1.72 $\pm$ 1.1	743	1.81 $\pm$ 0.9	871	Beach $\approx$ marsh	3.5	0.06
<b>Eggs abandoned</b>							
Both years	0.05 $\pm$ 0.3	1,647	0.03 $\pm$ 0.2	1,645	Marsh > beach	9.45	0.002
1986	0.03 $\pm$ 0.2	904	0.02 $\pm$ 0.2	775	=	0.9	ns
1987	0.07 $\pm$ 0.3	743	0.02 $\pm$ 0.2	871	Marsh > beach	8.9	0.003
<b>Eggs destroyed</b>							
Both years	0.15 $\pm$ 0.5	1,647	0.07 $\pm$ 0.3	1,645	Marsh > beach	28.8	0.0001
1986	0.23 $\pm$ 0.6	904	0.07 $\pm$ 0.3	775	Marsh > beach	44.0	0.0001
1987	0.05 $\pm$ 0.3	743	0.07 $\pm$ 0.3	871	=	0.6	ns

however, habitat did not consistently separate internest distances. Multiple comparison analysis indicated that Cedar Beach did not differ significantly from five marsh colonies, and several marsh colonies differed among themselves. West End 1 had internest distances significantly less than seven marsh colonies.

**Clutch size.** Clutches were larger in the marshes in both years (Table 2). This was primarily due to the relatively low mean clutch size at Cedar Beach ( $2.05 \pm 0.6$ ,  $n = 1,401$ ), which multiple comparison analysis showed to be significantly lower than both other beach colonies ( $2.20 \pm 0.6$ ,  $n = 641$  at West End 1 and  $2.40 \pm 0.7$ ,  $n = 34$  at West End 2), and significantly lower than Seganus, W. Fox, and East of West marshes. Mean pooled-year clutch size among marsh colonies ranged from  $2.10 \pm 0.7$  (Fishing Hat) to  $2.40 \pm 0.5$  (W. Gilgo). Thus, habitat alone did not determine clutch size.

**Egg volume.** Interhabitat differences in egg volume were not significant ( $F = 3.34$ ,  $df = 1$ ,  $P < 0.07$ ). Volume of eggs differed among colonies ( $F = 2.86$ ,  $df = 6$ ,  $P < 0.01$ ), but multiple comparison analysis indicated that the only significant differences that existed were that West End

1 (barrier beach) had greater egg volumes than Cedar Beach and Seganus marsh.

**Hatching success.** More eggs per nest hatched on beaches than in marshes, despite the smaller average clutch size on beaches (Table 2). Although strong overall interhabitat differences existed, again there were significant differences among colonies within habitats. Multiple comparison tests indicated that West End 1 (a beach) had significantly higher hatching success than Cedar Beach and six marsh colonies. Six marsh colonies had significantly greater hatching per nest than two other marsh colonies that had particularly low hatching rates (North Line and Fishing Hat). In addition, hatching success at Cedar Beach was significantly greater than three marsh colonies but not statistically different from five others (Tukey's multiple range test). Mean hatching success ranged from  $0.23 \pm 0.7$  at Fishing Hat in 1986 ( $n = 26$ ) to  $2.27 \pm 0.8$  at West End 1 in 1986 ( $n = 199$ ).

**Egg abandonment.** More eggs were abandoned in marshes than on beaches, an effect that is due primarily to differences in 1987 (Table 2). Again, habitat alone did not determine abandonment rates. Multiple comparison tests indicated that

TABLE 3. Interyear comparisons for Common Tern reproductive parameters from egg laying through hatching (see Table 2 for separate information on marshes and beaches).

	1986		1987		Rank order	F	P <
	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n			
<b>Clutch initiation</b>							
Both habitats	27 May $\pm$ 7	1,255	5 June $\pm$ 10	1,333	1987 > 1986	739.2	0.0001
Marshes	(see Table 2)				1987 > 1986	169.8	0.0001
Beaches					1987 > 1986	541.7	0.0001
<b>Clutch size</b>							
Both habitats	2.22 $\pm$ 0.6	2,175	2.13 $\pm$ 0.6	1,810	1986 > 1987	18.7	0.0001
Marshes					1986 > 1987	9.7	0.002
Beaches					1986 > 1987	4.0	0.04
<b>Eggs hatched</b>							
Both habitats	1.88 $\pm$ 0.9	1,679	1.77 $\pm$ 0.9	1,614	1986 > 1987	9.9	0.002
Marshes					=	0.1	ns
Beaches					1986 > 1987	41.9	0.0001
<b>Eggs abandoned</b>							
Both habitats	0.03 $\pm$ 0.2	1,679	0.05 $\pm$ 0.3	1,614	1987 > 1986	3.7	0.05
Marshes					1987 > 1986	6.1	0.01
Beaches					=	0.0	ns
<b>Eggs destroyed</b>							
Both habitats	0.15 $\pm$ 0.5	1,679	0.06 $\pm$ 0.3	1,614	1986 > 1987	35.4	0.0001
Marshes					1986 > 1987	47.7	0.0001
Beaches					=	0.2	ns

the mean pooled-year abandonment rate at West End 2 (a beach site) was significantly higher than both other beach colonies and six salt-marsh colonies. There was very high abandonment among the small number of remaining birds at the beleaguered West End 2 colony in 1987 (20% of nests). One salt-marsh colony (Tilted Log) had significantly higher abandonment (12%,  $n = 95$ ) than the East of West marsh colony and the two large beach colonies. None of the other marsh or beach colonies had abandonment rates that differed from one another (Tukey's multiple range test).

**Egg destruction.** More eggs were destroyed prior to hatching in marsh colonies than on beaches. This generalization resulted primarily from a between-habitat difference in 1986; there was no difference between habitats in 1987 (Table 2). Once again, the general difference among habitats was not consistently reflected in the inter-colony comparisons. For pooled data from both years, multiple comparison tests indicated that the only significant differences in egg destruction among individual colonies were that: (1) North Line (marsh) had significantly higher egg destruction than all other beach and marsh colonies, (2) Fishing Hat (marsh) had higher destruction than

all other colonies except N. Line, and (3) E. of West (marsh) had significantly higher nest destruction than Tilted Log (marsh) and West End 1.

**Interyear comparisons.** Year had a significant effect on most comparisons (Table 3). Birds in both habitats laid eggs significantly earlier and laid larger clutches in 1986 (Tables 2 and 3). The potential for larger broods that these larger clutches allowed was realized for beaches in 1986, but higher nest loss in marshes in 1986 caused the number of hatchlings per nest to be equal in marshes in both years (Tables 2 and 3).

**Nest substrate.** In marshes, of 1,869 nests for which we have data on nest substrate, 75% (1,402) were located on windrows of dead vegetation (hereafter mats) which were usually located near the edges of islands, and 25% (467) were located in high marsh areas on living salt-marsh hay, *Spartina patens* (and some spike grass, *Distichlis spicata*). This difference in distribution was highly significant (goodness of fit  $\chi^2 = 467$ ,  $df = 1$ ,  $P < 0.0001$ ). That terns select mats is emphasized by the fact that a high fraction of terns nested on them even though mats occupied only a small fraction of most islands. Mats are less vulnerable to flooding because they float in place in minor floods, whereas *S. patens*, being alive and rooted,

quickly becomes inundated during floods. Floods are usually caused by full or new moons, especially in conjunction with strong winds. Clutch-initiation date, clutch size, hatching rates, and nest-destruction rate varied significantly between substrates (Table 4). Despite a slightly larger clutch size on *S. patens*, more nests were destroyed there and consequently more chicks hatched per nest on vegetation mats than on *S. patens*. The later mean initiation date on mats (Table 4) reflects the fact that nests were initiated on mats throughout the egg-laying period, whereas nests were initiated on *S. patens* only during the peak of the egg-laying period (Fig. 4). Birds initiated nests on mats from 10 May through 3 July, whereas they initiated nests on *S. patens* from 16 May through 23 June.

Nests in salt marshes are built taller (distance from surface of nest substrate to nest rim) than in dry land colonies ( $F = 935, n = 200, P < 0.00001$ ). Nests were significantly taller on mats than on *S. patens* ( $F = 24.3, n = 111, P < 0.00001$ ) even though *S. patens* nests are more vulnerable to inundation. Thus, birds nesting on *S. patens* did not seem to compensate for the greater risk of flooding by building higher nests.

CHICK GROWTH AND SURVIVAL

We examined interhabitat differences in the wing length and weight of chicks at each day of age during the pre fledging period. Growth of all chicks (those surviving to fledging and those that died, pooled) was greater in beach colonies ( $n = 87$ ) than in marsh colonies ( $n = 57$ ) for wing length (Kolmogorov-Smirnov two-sample test,  $D = 0.14, P < 0.0001$ ) and weight ( $D = 0.17, P < 0.0001$ ). However, growth of chicks that survived ( $n = 40$  on beaches, 15 in marshes) was not significantly different between habitats for either wing length ( $D = 0.06, ns$ ) or weight ( $D = 0.06, ns$ ). At fledging, chicks showed no differ-

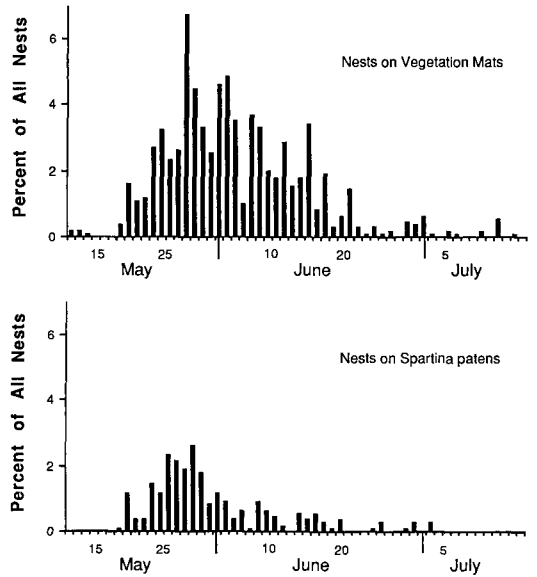


FIGURE 4. Phenology of clutch initiation on different substrates in marsh colonies. Percents refer to the total number of nests in marshes.

ences in wing length ( $F = 2.3, ns$ ) or weight ( $F = 1.0, ns$ ), either between habitats or between the two larger beach colonies.

In beach colonies, 143 chicks hatched and 84 fledged from 69 nests in 14 fences in 1986 and 87 chicks hatched and 40 fledged from 64 nests in eight fences in 1987. In marshes, 70 chicks hatched and 41 fledged from 38 nests in seven fences in 1986 and 57 chicks hatched and 20 fledged from 27 nests in eight fences in 1987. There was no significant difference between habitats in the number of chicks fledged per egg laid ( $F = 0.5, P < 0.5$ ), per egg hatched ( $F = 1.3, P < 0.3$ ), or per nest ( $F = 0.003, P < 1$ ) for pooled fence data from both years. This was also true in 1986 and 1987 separately.

Survival was greater in 1986 than in 1987 in both habitats (Tables 5 and 6). In the beach col-

TABLE 4. Comparisons of Common Tern nests on dead vegetation mats and on living *Spartina patens* in salt marshes.

	Mat		<i>Spartina patens</i>		Rank order	F	P <
	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n			
Initiation date	30 May $\pm$ 9	840	27 May $\pm$ 8	274	Mat > <i>Spartina</i>	23.0	0.0001
Clutch size	2.23 $\pm$ 0.6	1,411	2.31 $\pm$ 0.6	458	<i>Spartina</i> > mat	4.2	0.04
Eggs hatched	1.76 $\pm$ 1	1,220	1.59 $\pm$ 1	393	Mat > <i>Spartina</i>	8.1	0.004
Eggs abandoned	0.05 $\pm$ 0.3	1,220	0.04 $\pm$ 0.3	393	=	0.6	ns
Eggs destroyed	0.13 $\pm$ 0.5	1,222	0.20 $\pm$ 0.6	391	<i>Spartina</i> > mat	4.8	0.03

TABLE 5. Numbers of Common Tern chicks surviving to fledging per nest among the two large beach colonies, Cedar Beach (CB) and West End 1 (WE), and salt marshes. *n* = number of nests.

	Cedar Beach		West End 1		Marshes	
	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>
No. fledged per:						
Egg laid						
Both years	0.55 ± 0.33	71	0.39 ± 0.41	62	0.44 ± 0.37	65
1986	0.53 ± 0.28	40	0.68 ± 0.36	29	0.52 ± 0.36	38
1987	0.58 ± 0.39	31	0.13 ± 0.23	33	0.31 ± 0.33	27
Egg hatched						
Both years	0.60 ± 0.33		0.52 ± 0.42		0.50 ± 0.40	
1986	0.56 ± 0.25		0.70 ± 0.37		0.62 ± 0.36	
1987	0.65 ± 0.38		0.32 ± 0.47		0.34 ± 0.35	
Nest						
Both years	1.06 ± 0.58		0.79 ± 0.87		0.94 ± 0.77	
1986	1.07 ± 0.52		1.41 ± 0.78		1.08 ± 0.80	
1987	1.03 ± 0.72		0.24 ± 0.45		0.74 ± 0.71	

\* Cedar Beach is not significantly different from the marshes, and the marshes are not significantly different from West End 1, but Cedar Beach is significantly greater than West End 1.

onies, this difference was largely due to heavy predation, mostly by Herring Gulls (*Larus argentatus*), at West End 1 in 1987. Gulls also appeared to be much more active in marshes in 1987 (see next section on Flooding, Disturbance and Predation).

#### FLOODING, DISTURBANCE AND PREDATION

Marsh-nesting terns must contend with floods and avian predators. High tides on 23 May 1986 left most islands wet and caused the immediate abandonment of one slightly inundated island where almost 300 terns had not yet laid eggs but had begun to defend against intruders. A flood on 13 June 1986 caused much chick mortality, but was early enough in the season that it affected only a small percentage of the season's chick cohort (see next paragraph). Flooding on 14 July 1987 wet many marsh nests but did not contribute much to mortality.

Examining the 13 June 1986 event in detail illustrates the role of timing in determining the impact of a flood on overall productivity in marshes. At the time of the flood, 85% of the season's clutches were laid, but only 16% of them had begun hatching, and only 18% of the season's total chicks had hatched. Of 955 nests active prior to the flood, 100 nests experienced egg loss and 75 nests had dead hatched or pipping chicks as a result of the flood. The flood killed 51% of the chicks that had hatched up to that date, and 62% of the chicks that were alive when the flood occurred, but only 9% of the total number of

chicks that hatched in marshes in 1986 were killed in this event. This accounted for 47% of the total marsh chick mortality for the season. The flood killed 51% of the eggs that were pipping, and accounted for 55% of the season's mortality of chicks which died while pipping. If one combines hatched and pipping chicks, the flood killed 11% of the season's total marsh chicks, and accounted for 48% of the season's mortality in marshes. If the flooding had occurred just after the peak of hatching, it would have been much more destructive.

Herring Gulls nested in several marsh colonies in 1986, but in 1987 gull activity increased. Gulls appeared to displace terns from one marsh islet. West Gilgo experienced heavy predation in 1987, perhaps from an owl; head, wings, and feet of chicks were left in the colony.

Beach-nesting terns are usually not flooded, but they must contend with mammalian predators, humans, and avian predators. Gulls caused relatively little destruction at the two larger beaches in 1986. We observed predators from blinds in the course of early morning observations (dawn to 09:00 every other day from late June through late July) of chicks in both years at Cedar. In 1986, within our very limited view from the blind we saw gulls in the colony approximately 20 times, and two chicks were seen to be taken by them. Northern Harriers (*Circus cyaneus*) were seen in the colony seven times, but were not seen to take chicks. In contrast, in 1987 during a similar period of early morning



TABLE 5. Extended.

Rank order	F	P <
CB (=Marsh=) > WE*	3.6	0.03
=	2.1	ns
CB > Marsh = WE	15.1	0.0001
=	1.1	ns
=	1.2	ns
CB > Marsh = WE	6.0	0.004
=	2.1	ns
=	2.5	ns
CB = Marsh > WE	13.2	0.0001

observations, gulls were observed in the colony approximately 60 times, and took 24 chicks. Harriers entered the colony 18 times during our observations, and took seven chicks. At West End 1 a 15-pair gull colony became established at the eastern edge of the tern nesting area in 1987. Their depredations on both Common and Least terns in the colony were largely responsible for the severely reduced fledging success we measured there in 1987.

Mammals, including humans, appeared in beach colonies several times. In 1986 there was a weasel den at West End 1, and automobile tire tracks were found several times. In 1987 both automobile and bike tracks were found in the colony. At Cedar in 1986 tire tracks were found

one morning, and approximately 20 chicks had been crushed. Human tracks appeared several times, and people appeared in the colony several times but caused little damage.

COLONY-SITE SELECTION IN MARSHES

Areas of dead vegetation mats were greater on islands with nesting birds than without nesting birds ( $F = 5.2, df = 1, P < 0.02$ ). Using a stepwise regression model to compare the number of nesting pairs of terns and physical features of islands, we found a significant positive relationship between the number of pairs and the area of dead vegetation mats ( $F = 7.3, df = 29, P < 0.01$ ), as well as the distance from deeper channels ( $F = 7.7, df = 29, P < 0.01$ ). Other variables which were included in the regression analysis but did not contribute significantly to the model were island area, mean depth around islands, distance to nearest island, percent of island perimeter exposed to open bay, distance across open bay to other nearest land, direction of maximum exposure to wind and waves, and direction of minimum exposure. We did not find terns nesting in the extensive marshes contiguous with the barrier beach.

INTERCOLONY MOVEMENT

We analyzed the movements of 250 banded birds which we have recaptured since 1982 in the study area. Seventy-six percent of all recaptured birds were encountered in the same type of habitat where they were originally banded; this included 82% of the birds banded as adults and 66% of the birds originally banded as chicks, and was highly different from random movement ( $2 \times 2$

TABLE 6. Interyear comparisons of numbers of Common Tern chicks surviving to fledging per nest in both beach colonies and all salt marshes.

	1986		1987		Rank order	F	P <
	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$	n			
<b>Beaches</b>							
No. fledged per:							
Egg laid	0.59 ± 0.33	69	0.35 ± 0.42	64	1986 > 1987	15.4	0.0001
Egg hatched	0.62 ± 0.32		0.51 ± 0.43		=	2.4	ns
Nest	1.21 ± 0.72		0.63 ± 0.72		1986 > 1987	25.1	0.0001
<b>Marshes</b>							
No. fledged per:							
Egg laid	0.52 ± 0.36	38	0.31 ± 0.33	27	1986 > 1987	5.2	0.03
Egg hatched	0.62 ± 0.36		0.34 ± 0.35		1986 > 1987	8.7	0.005
Nest	1.08 ± 0.80		0.74 ± 0.71		1986 = 1987	3.2	0.09

contingency table with Yates correction for continuity,  $\chi^2 = 69.59$ ,  $P < 0.001$ ). Of 206 recaptured birds which had been banded on beaches, 78% were recaptured on beaches ( $2 \times 2$  contingency table with Yates correction,  $\chi^2 = 62.98$ ,  $P < 0.001$ ). Of 44 recaptured birds which had been banded in marshes, 70% were recaptured in marshes ( $2 \times 2$  contingency table with Yates correction,  $\chi^2 = 7.28$ ,  $P < 0.01$ ).

Birds banded as chicks were slightly more likely to be found breeding in a different habitat than birds banded as breeders. Sixty-six percent of 88 recaptured birds originally banded as chicks were found breeding in the same type of habitat they hatched in, whereas 82% of 162 recaptured birds banded as breeding adults were subsequently found breeding in the same type of habitat. This was different from random movement for both birds banded as chicks ( $\chi^2 = 8.85$ ,  $P < 0.01$ ) and birds banded as adults ( $\chi^2 = 66.64$ ,  $P < 0.001$ ).

Of 162 birds banded as adults, birds originally found breeding on beaches were recaptured on beaches 82% of the time, and birds originally found breeding in marshes were recaptured in marshes 82% of the time as well. Thus, birds breeding in each habitat are equally likely to breed in that habitat subsequently.

Of birds banded as chicks, 70% of 77 birds hatched on beaches were recaptured on beaches, and 50% of 16 birds hatched in marshes were recaptured in marshes. Thus, chicks hatched on beaches are likely to breed on beaches ( $\chi^2 = 10.81$ ,  $P < 0.01$ ). We are hesitant to conclude anything about the subsequent movement of chicks hatched in marshes because of the small sample.

## DISCUSSION

Salt marshes have been viewed as suboptimal breeding sites for Common Terns (Burger and Shisler 1979, Buckley 1979, Erwin et al. 1981). Three main arguments have been advanced to support this view: (1) Recent patterns of human coastal development correspond with patterns of recent marsh use by terns, (2) marsh nests are frequently destroyed by flood tides, whereas beach nests seldom are, and (3) terns nesting in marshes may be more vulnerable to avian predation than beach-nesting terns. Alternatively, marsh and beach nesting may both be similarly viable strategies evolved by this species for nesting in a system of inherently unstable environments. We review and discuss these arguments below.

## MARSHES AS RECENTLY COLONIZED HABITAT

Buckley and Buckley (1976) viewed marsh nesting by Common Terns as a habitat preference change, although Buckley (unpubl.) and Burger (1979) mentioned that Common Terns had made at least limited use of New Jersey marshes for more than a century (e.g., Wilson 1854, Stone 1937). Burger and Shisler (1979) and Buckley and Buckley (1980) concluded that human development of barrier islands had forced many previously beach-nesting birds onto salt marshes. Buckley and Buckley (1980) made a strong argument for the view that terns were being increasingly forced into marshes by noting that between 1974 and 1978 "the percentage of marsh-nesting Common Terns increases as the total Long Island Common Tern population increases." But they later (1982b) modified their earlier statement by saying that between 1974 and 1978 "the number of pairs in marshes each year were highly correlated with the total L.I. breeding populations." The latter statement suggests that there was not an increasing preference for salt marshes among Long Island Common Terns during the 1970s.

Erwin (1980) noted that in Virginia (where beaches were mostly protected) 80% of seabirds nested on beaches but that in New Jersey (where beaches are largely developed) the vast majority nested in marshes, as Burger and Lesser (1978) had found. It must be recognized, though, that where beaches are now fully developed and unavailable to birds, the fact that the majority of terns nest in marshes does not eliminate the possibility that many terns nested in marshes historically when beaches were also available. Erwin felt that barrier islands seemed to be preferred by terns and that urbanization had "presumably caused habitat shifts." Erwin et al. (1981) expanded some of these themes, especially that marsh nesting was a new phenomenon. Saying that many Common Terns had recently (in the last 30–50 years) moved away from traditional beach habitats, they described the "shift" from dry sandy beaches to wet vegetated marshes as an "abrupt change." Erwin et al. (1981) commented on the ability of Common Terns to "adjust rapidly" to the "new nesting conditions" in marshes by building taller nests there. We think it is more parsimonious to view nest building as

part of the behavioral plasticity which has evolved in this species over a long period of breeding under varied and inherently unstable conditions in salt- and freshwater systems.

An historical lack of comparable census data from salt marshes (Erwin 1980) makes the argument that marshes were little used historically a circumstantial one. Ornithologists were surprised to discover large numbers of Common Terns nesting in marshes (Burger and Lesser 1978, Buckley and Buckley 1980), but the lack of published reports of terns using marshes, rather than an actual scarcity of marsh-nesting terns, may have been responsible for the view that marsh nesting was uncommon. For instance, Erwin (1980) commented that marshes were used extensively for nesting by Common Terns only in New Jersey. This remark likely reflects the fact that Burger's censuses of the New Jersey marshes had been published in the late 1970s, while the Buckley's report of salt-marsh nesting on Long Island (1980) had not yet appeared in print. The Buckley's had found large numbers of Common Terns in Long Island marshes when they began censusing in 1973.

#### MARSHES AS SUBOPTIMAL HABITAT

Most researchers have viewed marshes as sub-optimal habitat in which birds face several problems not encountered on beaches. High storm tides often curtail the breeding efforts of birds nesting on salt-marsh islands (Burger and Lesser 1978, 1979; Burger 1982; Buckley and Buckley 1982a; Erwin and Smith 1985). This problem is seldom encountered by beach-nesting terns, although it can occur in some areas (Erwin and Smith 1985).

Burger and Lesser (1978) believed flooding to be the main disadvantage to marsh nesting. Further, while birds whose nests were destroyed at beach colonies frequently re-nested (Nisbet 1973), Burger and Lesser (1979) reported that terns which lost their nests to flooding on salt marshes frequently did not. But despite some flooding, marsh-nesting terns have repeatedly been found to be successful. Greenhalgh (1974) and Buckley and Buckley (1982a) found high survival of nests (70–95%) in marshes. Burger and Lesser (1979) reported that the effect of tides on marsh nests varied among colonies, and that even in a disastrous tide year seven of 11 colonies produced young.

Attempts to increase the productivity of marsh colonies would primarily involve efforts to reduce flooding risk and decrease avian predation (Herring and Black-backed gulls are a relatively recent predatory presence in mid-Atlantic marshes; see Burger and Lesser 1978). We found that the number of pairs of nesting birds was related to the area of vegetation mat present on islands. Increasing the area of mats would provide more nesting substrate where substrate is a limiting factor, and would buffer nests against flooding. This could allow more birds to nest and may thus also increase their effectiveness in predator defense. Increasing the height of mats would make marsh colonies even more resistant to flooding. Adding dredge spoil consisting of sand and shell fragments to marsh islands increases their attractiveness to several species of terns, but vegetation succession at such sites favors gulls and wading birds in the long-term (Erwin 1980), and greatly changes the marsh habitat for other species. Spoil sites would require occasional maintenance or addition of spoil to reverse vegetation succession. If dredge spoil is used, it should have a shell and sand surface, rather than a surface of pure sand, pure shell, silt, or mud. This would provide a relatively stable surface in which vegetation would not grow rapidly, and it would allow birds to make scrapes and not cause eggs to become stuck when the surface is wet. Deposition of spoil should be accomplished soon after the nesting season to allow for settling and to allow for some vegetation growth for chick cover (Soots and Parnell 1975, reviewed in Kotliar 1984). Shelter should be provided if the site is bare just prior to the terns' spring arrival. Any spoil island accessible by boat can be expected to be used by recreationalists for picnicking, camping, etc. Thus the best management scheme might be the one involving the least technology: manipulation of vegetation mats. This would leave the islands unattractive to people, relatively unaltered for other marsh species, and safer for terns.

#### RELATIVE PRODUCTIVITY OF BEACHES AND MARSHES

One may assess the relative viability of habitats from two different perspectives. In an evolutionary sense, the relative importance is best understood by measuring the number of young produced per pair as an index of fitness (Williams

TABLE 7. Common Tern productivity estimates (young fledged per nest).

Young per nest*	Habitat	Location	Source
0-0.96 (mean 0.2)	Salt marsh	New Jersey	Burger and Lesser 1978
0.65-1.03	Salt marsh	Great Britain	Greenhalgh 1974
0-1.36 (means 0.69/0.27)	Salt marsh	New Jersey/Virginia-Maryland	Erwin and Smith 1985
0.59, 1.08 (annual means)	Salt marsh	Long Island, New York	This study
0.9-1.1	Beach	Massachusetts	Nisbet 1973, 1978
0-1.83 (mean 0.82)	Beach	New Jersey-Virginia-Maryland	Erwin and Smith 1985
0.63, 1.21 (annual means)	Beach	Long Island, New York	This study

\* Methods of estimation vary and are not strictly comparable.

1966, Ricklefs 1969). From a management perspective, we may ask how much each habitat contributes to the regional population (fitness  $\times$  number of pairs), and how that might be manipulated.

Several authors have recently commented on reproductive output per pair ("fitness") in each habitat. The weight of published opinion has changed since 1980, when the relative success of reproduction in beach and marsh habitats was generally considered to be unknown (Erwin 1980) and it was largely assumed that marshes were not very productive (perhaps partly because chicks vanish in marsh grass and are much more apparent at beach sites). Buckley and Buckley (1982a) acknowledged that "contrary to recent comments on the sub-optimal nature of salt-marsh-nesting sites (cf. Buckley 1979, Buckley and Buckley 1980, Erwin et al. 1981), Common Terns are able to cope successfully with marsh conditions . . . and have been doing so for some time." They also (Buckley and Buckley 1982b) found no significant differences between habitats in terms of colony establishment or abandonment, and felt that for the years of their study marshes were as successful as beaches. Erwin and Smith (1985), comparing productivity data from different areas of the coast over several years, found no consistent effect of habitat on the number of fledglings per pair, and much variability among colonies and years. They report that the effects of interyear differences were great enough to mask any differences due directly to habitat. Our results concur. The differing rates of egg survival and hatching that we found suggest that birds in marshes are at a slight disadvantage, but the number and health of young fledged per pair per season did not differ between habitats.

Several other productivity estimates for Common Terns have shown considerable overlap between dry land and marsh sites in various places

(Table 7). Thus the data indicate that, from an evolutionary viewpoint, marshes are viable and productive breeding sites for Common Terns. From a manager's point of view, their contribution to populations varies regionally. Major erosion or development of beaches would increase the relative importance of marshes. Buckley and Buckley (1982b) hypothesized that marshes provided the refugia for relict populations that prevented extirpation of Common Terns in the late 1800s.

#### MARSHES AS TRADITIONAL SITES

Buckley and Buckley (1980) noted that prior to their flights over Long Island the phenomenon of marsh nesting by Common Terns was believed rare, but acknowledged that Alexander Wilson's familiarity with marsh-nesting Common Terns as early as the 1830s (Wilson 1854) had been overlooked by some subsequent authors. Comparisons with other terns may be instructive in assessing the degree to which Common Terns are adapted to marsh nesting. Common Terns build nests similar to Forster's Terns (*Sterna forsteri*), which are marsh specialists (Storey 1978 in Erwin et al. 1981). Least Terns (*S. antillarum*) do not use salt marshes for nesting, despite (1) their frequent use of marsh areas for foraging, (2) considerable pressure on their habitat which has resulted in serious population declines (on Long Island there is more human recreation pressure on Least Tern habitat than on Common Tern habitat; Safina, pers. observ.), (3) their use of sandy spoil areas on islands which had been marshes prior to spoil deposition, and (4) their recent use, apparently in response to habitat destruction, of several alternate habitats: spoil piles, paved streets, roofs, and airports (Altman and Gano 1984, Kotliar 1984). In New Jersey, where Common Terns are thought to have been forced onto marsh islands, but do not nest on the main-

TABLE 8. Advantages and disadvantages of nesting on beaches, in marshes contiguous with the mainland or barrier beaches, or on marsh islands.

	Beaches	Marshes contiguous with mainland or barrier beaches	Marsh islands
Main advantages	Floods are rare	None	Fewer mammals
Main disadvantages	Mammals common	Flooding, mammals common	Flooding common

land (Burger and Lesser 1979), Least Terns never nest in marshes but nest on spoil piles on the mainland (Kotliar 1984). Roseate Terns (*S. dougallii*) on Long Island have nested in salt marshes, but are seldom successful there (Buckley and Buckley 1980). It seems probable that Common Terns are successful in salt marshes because they are better adapted to nesting in them than are some other terns.

Erwin et al. (1981) tested the prediction that traditional marsh nesters (Forster's Terns and Laughing Gulls, *Larus atricilla*) were more consistent in site from year to year than marsh "invaders" (Common Terns, Herring Gulls, Black Skimmers, *Rynchops niger*). "Presumably, the latter species have not had sufficient time to acquire fine-tuned adaptations and, hence, are possibly inferior in judging high quality sites in marshes." But the results did not support the prediction that colony-site change should be lower for marsh specialists than invader species in marsh habitats. While we agree that Forster's Terns and Laughing Gulls are marsh specialists and the other species are not, we see these results as supporting the view that Common Terns are not new invaders but rather well adapted to the contingency of marsh nesting.

Although terns may seem to prefer beaches when these are available and predator pressure there is not too heavy (Erwin and Smith 1985), this preference does not seem strong. On Long Island, for instance, considerable numbers of terns nested in the marshes at least as early as the mid-1970s, when there was much available habitat on beaches; Cedar Beach contained half as many pairs as it did during the present study, and the beach at West End 1 was not yet colonized by Common Terns. If terns strongly preferred beaches, we would expect these sites to reach maximum density before birds went elsewhere, but Erwin and Smith (1985) reported that nest spacing was much closer in salt marshes than on beaches. We found that nests were closer together on beaches. Nest spacing may relate more to space limitation and predation pressure than habitat

per se. The conflict between our result and that of Erwin and Smith suggests that there is not a strong preference for one habitat. Further, terns banded in the late 1970s as breeders at Cedar Beach subsequently bred on marshes and at other beach sites rather than remaining in the Cedar colony (Gochfeld 1979). Buckley and Buckley (1980) similarly noted that individual Common Terns move from marsh to beach and back again between nesting attempts. Burger (pers. comm.) found a bird nesting in New Jersey marshes which had been trapped on a nest at Cedar Beach earlier in the same season. Our analysis of movements of banded birds indicates that birds tend to return to breed in the same habitat in which they were hatched and that breeding adults in each habitat are equally likely to nest subsequently in the same habitat, suggesting no strong species-specific preference for one particular habitat.

We did not find terns nesting in the extensive marshes contiguous with the barrier beach. Burger and Lesser (1978) likewise did not find terns in very extensive marshes contiguous to the mainland or beaches along 46 miles of New Jersey coast. When nesting in salt marshes, then, terns nest only on salt-marsh islands. If terns were indeed moving to marshes only because they were displaced from beaches, we might expect them to colonize marshes near their former beach colonies, or near inlets, which is where beach colonies are often located (Buckley and Buckley 1980). They do not do this, however. Their use of marsh islands instead of marshes contiguous to large land masses appears to be a habitat choice and further supports the notion that marsh nesting represents an alternative strategy rather than a lack of options. Although birds nesting in marshes often avoid relatively heavy mammalian predation (we found no evidence of mammalian predation on marsh islands in our study), they must contend with the stress of flooding (Buckley and Buckley 1982a, Burger 1985). Tabulation of the primary advantages and disadvantages of nesting on beaches, on marsh islands, or in marshes contiguous with mainland

or barrier islands suggests that the latter situation is the only one that offers no advantages, while nesting on beaches or marsh islands offers reciprocal advantages and disadvantages (Table 8).

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